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CONSEQUENCES OF PLANT RESISTANCE FOR HERBIVORE SURVIVORSHIP, GROWTH, AND SELECTION ON EGG SIZE

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Abstract. Plants can vary substantially among species in morphological and physiological traits that influence their resistance to herbivores and their quality for herbivore growth and development. Seeds of the desert trees *Cercidium floridum* and *C. microphyllum* vary within and among populations in their resistance to, and suitability for, growth and development of larvae of the seed beetle, *Stator limbatus*. We examined how this variation influences the magnitude of natural selection on the size of eggs laid by beetles and tested whether female beetles can distinguish between seeds of more vs. less suitable trees (within species). We found that selection favoring large eggs differed substantially between the two tree species (greater on *C. floridum*) and varied substantially among populations of *C. floridum* and among trees (within populations) of both *C. floridum* and *C. microphyllum*. In general, the magnitude of selection favoring large eggs correlated positively with seed coat resistance between tree species, among populations within species, and among trees within populations. Female *S. limbatus* are capable of distinguishing seeds of the two host species and respond to species differences in selection by laying larger eggs on seeds of *C. floridum* than on seeds of *C. microphyllum*. However, despite large variation in seed suitability within populations of trees, females did not preferentially lay eggs on seeds of less resistant trees, nor did they adjust egg size in response to variation in resistance among trees.

Key words: body size; Cercidium; *development time; egg size; natural selection; oviposition preference; paloverde; selection intensity;* Stator limbatus; *survivorship.*

INTRODUCTION

Plants can vary substantially among species in morphological and physiological traits that influence their resistance to herbivores and their quality for herbivore growth and development (Fritz and Simms 1992, Kennedy and Barbour 1992, Weis 1992). Plant resistance and quality can also vary substantially among populations (Singer and Parmesan 1993) or among individuals within populations (Karban 1992, Larsson and Strong 1992), and this variation can influence herbivore distributions (Pilson 1992, Karban and Kittelson 1999). This variation can also influence the evolution of herbivore morphological, physiological, behavioral, and life history traits (Rausher and Papaj 1983, Fox et al. 1997*a*) by increasing the variation in natural selection experienced by herbivores. Variation in selection may limit the ability of herbivores to adapt to their host plants because the characters that improve performance on one individual plant may be different from the characters that improve performance on another individual plant. Alternatively, herbivores may adapt to specific plant genotypes within a population (Karban 1989, Komatsu and Akimoto 1995).

The substantial variability among plants within a population also selects for the ability of herbivores to distinguish more suitable from less suitable individuals when feeding or ovipositing. When comparing among plant species, there is often concordance between the plants that herbivores prefer to eat or oviposit upon and the plants upon which they develop best (Nylin and Janz 1993, Janz et al. 1994, Barros and Zucoloto 1999, Poore and Steinberg 1999) although there are a large number of exceptions (Kibota and Courtney 1991, Pawlitz and Bultman 2000, reviews in Thompson 1988, Fox and Lalonde 1993, Mayhew 1997). Fewer studies have examined insect preferences for individual plants within a single species (Singer and Lee 2000) and have found mixed results (Quiring and Butterworth 1994). In most studies, females exhibit preferences for some individual plants over others but these preferences are not concordant with plant suitability for offspring growth (Mackay 1985, Karban and Courtney 1987, Valladares and Lawton 1991, Larsson and Strong 1992, Zangerl and Berenbaum 1992, Underwood 1994). A few studies have found that females do preferentially oviposit on more suitable plants (Rausher and Papaj 1983, Leather 1985, Ng 1988, Anderson et al. 1989, Brody and Waser 1995). We know of no studies that have failed to find variation among plants within a population in their acceptability for oviposition by female herbivores.

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Here we quantify variation among species, among plant populations (within species), and among individual plants (within populations) in resistance to larvae, and suitability for larval growth and development, of a seed beetle (*Stator limbatus*; Coleoptera: Bruchidae). *Stator limbatus* is a generalist seed parasite (Johnson and Kingsolver 1976, Johnson et al. 1989, Nilsson and Johnson 1993) that is abundant on seeds of numerous plant species including two species of paloverdes, *Cercidium floridum* (Benth.) and *C. microphyllum* (Benth.) in the southwestern United States. Seeds of these two paloverdes differ substantially in their suitability as substrates for beetle development (Siemens and Johnson 1990, Siemens et al. 1992, Fox et al. 1996). Egg-to-adult survivorship is very low when larvae develop on *C. floridum* (generally <50%) relative to *C. microphyllum* (generally >80%), and egg-to-adult development time on *C. floridum* is 4–6 d longer (28–30°C) than on *C. microphyllum* (Fox et al. 1996). In part, these differences result from differences between species in chemically based seed defense mechanisms (Siemens et al. 1992). These two *Cercidium* species are often sympatric, but there are many regions where only one or the other species is present.

Differences in seed coat defenses between *S. limbatus* host species result in differences in natural selection on egg size. This has been demonstrated for the comparison of larvae developing on seeds of *C. floridum* vs. *Acacia greggii*, another desert perennial (Fox and Mousseau 1996). Natural selection favors females that lay large eggs when their larvae will develop on seeds of *C. floridum* (because larvae hatching from large eggs can penetrate the seed coat whereas larvae from small eggs cannot), but selection favors females laying much smaller eggs on *A. greggii* (because larvae from small eggs can successfully penetrate the seed coat, and females laying small eggs have higher fecundity than females laying large eggs; Fox and Mousseau 1996, Fox et al. 1997*a*). Apparently in response to this variation in seed coat defenses, and the corresponding variation in natural selection on egg size, *S. limbatus* has evolved egg size plasticity in which females lay larger (and fewer) eggs on *C. floridum* than on *A. greggii* and can switch between small and large eggs when rotated among host plants (Fox et al. 1997*a*, 1999, Fox and Savalli 2000). Because *C. microphyllum* is a high-quality host relative to *C. floridum* (*C. microphyllum* is similar in suitability to *A. greggii*), it is likely that selection on egg size is relaxed on this host, with natural selection favoring females that lay larger eggs on *C. floridum* than on *C. microphyllum*. However, natural selection on *C. microphyllum* and female responses to this host have not yet been examined.

Trees can also vary in resistance within populations, producing substantial variation in selection on egg size (Fox 2000). This variation in selection is expected to result in the evolution of larger progeny than predicted by models that assume low variance in selection on progeny size (Forbes 1991, Lalonde 1991). Variability in selection can also favor the evolution of increased variance in progeny size within families (McGinley et al. 1987, Philippi and Seger 1989) or plasticity in progeny size (Clutton-Brock 1991, Roff 1992). However, few studies have examined the amount of variation in selection on egg size within populations (but see Nakasuji and Kimura 1984, Braby 1994, Sinervo 1998, Fox 2000).

Here we quantify variation among populations of *C. floridum* and among individual plants (within populations) of both *C. floridum* and *C. microphyllum* in resistance to, and suitability for, growth and development of *S. limbatus* larvae. We then examine variation in the magnitude of natural selection on egg size between host species and among individual trees within populations to test the hypothesis that the magnitude of natural selection on egg size increases as seed coat resistance increases. Last, we examine whether female *S. limbatus* distinguish between seeds of more vs. less suitable trees (within species) by either (1) laying larger eggs on seeds of less suitable trees (examined for both *C. floridum* and *C. microphyllum*) or (2) preferentially ovipositing on the seeds of more suitable trees (examined for *C. floridum*).

METHODS

Natural history of Stator limbatus

Stator limbatus oviposits directly onto host seeds and is thus restricted to seed pods that have either dehisced or been damaged by other organisms. For hosts that are indehiscent, such as *C. floridum*, beetles attack seeds almost entirely through emergence holes in the pod caused by other bruchids, such as *Mimosestes* spp., which oviposit on host legumes (fruits) rather than directly on seeds (Siemens et al. 1992). In dehiscent hosts, such as many *Acacia* species, beetles will attack both dehiscing pods and pods damaged by other insects (C. W. Fox, *personal observation*).

Upon hatching, larvae burrow into the seed directly under the egg. They complete development and pupate inside the seed, and emerge from the seed as adults. Beetles require only a single seed to complete development and reproduce. Adults are the only dispersing stage; larvae are restricted to the host their mother has chosen for them. In the laboratory, mating and egg laying begin ~24–48 h post-emergence.

Further details on the ecology of these beetles and their host plants can be found in Fox et al. (1994, 1995), Siemens and Johnson (1990), and Siemens et al. (1992, 1994).

Study populations

For all experiments, beetles and seed stock were collected by picking mature seed pods from >10 (generally >25) *C. floridum*, *C. microphyllum*, or *Acacia greggii* plants. Mature pods were transferred to the laboratory, and seeds containing beetles were separated from uninfested seeds. Adult beetles emerging from these field-collected seeds were used to initiate our laboratory populations. We estimate that all laboratory *S. limbatus* populations were initiated with >300 field-collected individuals. These beetles were reared in the laboratory on a common nonpaloverde host, *Acacia greggii* (a natural host for *S. limbatus* in Arizona and California), for at least one generation at 30°C, L:D 15:9 (i.e., a photoperiod of 15 h light and 9 h dark), to control for maternal effects (Fox et al. 1995). We used seeds of *A. greggii* for most laboratory rearing because larval mortality is very low on this host (generally <5%) and thus the opportunity for natural selection on this host is low relative to other hosts.

Seeds were collected from various populations of *C. floridum* and *C. microphyllum* (details are provided for each experiment). Seeds containing entrance or emergence holes of other bruchids (such as *Mimosestes* spp.) were discarded; only undamaged seeds were used for rearing beetles in the laboratory experiments.

Definitions

For consistency throughout the paper, seed coat ''resistance'' refers to the proportion of *S. limbatus* larvae that die (i.e., mortality) as they attempt to penetrate the seed coat of a *C. floridum* or *C. microphyllum* seed. Thus resistance is a property of both the insect and plant. It is affected by both the defenses present on the seed and the phenotype (e.g., egg size) of the insect feeding on that seed.

The ''suitability'' of seeds for the development of larvae refers to (1) the survivorship of larvae after seed coat penetration until adult emergence, (2) total egg-to-adult survivorship of larvae, (3) egg-to-adult development time, and (4) the body mass of beetles at adult emergence. Note that egg-to-adult survivorship is a function of both larval mortality during seed coat penetration coat and the survivorship of larvae within seeds.

Seed coat resistance, beetle growth and survivorship, and selection on egg size: variation among trees within a population

This first experiment was designed to (1) quantify differences between *C. floridum* and *C. microphyllum*, and (2) quantify variation among individual trees within each species in both the resistance of their seeds to larval penetration and the suitability of their seeds for larval development. We also examined the influence of female egg size on larval survivorship and growth, and tested whether this influence differed among trees.

Beetles were collected on 15 July 1995 from seeds of *C. floridum, C. microphyllum*, and hybrids of these two paloverdes along Highway 62 and Old Parker Dam Road near Earp, San Bernadino County, California (referred to as the Earp population). The beetles were reared in the laboratory for a single generation on seeds of *A. greggii* at 30°C, L:D 15:9, before the start of these experiments.

To create families of beetles, virgin males and females were collected from isolated seeds of *A. greggii* within 12 h of adult emergence. Each was weighed and then paired with a single virgin of the opposite sex. Each pair was confined in a 35-mm petri dish containing either (1) 12 *C. floridum* seeds, or (2) 12 *C. microphyllum* seeds. All seeds within a dish were collected from a single tree chosen from 10 *C. floridum* and 10 *C. microphyllum* plants from which seeds were harvested in the field. Dishes were checked for eggs every 12 h until the female had laid an egg on each of 10 or more seeds. At each census time the seeds bearing eggs were removed from a dish so that the time at which each egg was laid was known to be within the preceding 12 h period.

The size of the eggs that females laid (egg length and width) was recorded for eggs laid within the first 12 h after egg laying was initiated. 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 and Mousseau 1996). It is not practical to weigh eggs because they are glued to seeds making their removal very time consuming and often destructive.

All larvae were reared to adult at 30°C, L:D 15:9, at densities of one larva/seed (eggs in excess of one per seed were removed from the seed). Egg-to-adult development time and adult body mass at emergence were recorded for all progeny. Seed coat resistance was quantified as: 1 − the proportion of larvae that successfully penetrated the seed coat. Larvae that successfully penetrate the seed coat fill the egg with white frass (feces) while those that die are visible in the egg with their sclerotized head partially penetrating the seed coat. A larva was thus classified as having failed to penetrate if it died with any part of its abdomen still protruding from the seed coat. Eggs that do not develop can be identified by the lack of a larva. Eggs that develop but do not hatch can be identified by the failure of the larva to start burrowing into the seed coat. Larval survivorship within seeds (survivorship from seed coat penetration until adult emergence) and total egg-to-adult survivorship were also recorded for each family.

Mortality of larvae on *C. floridum* is nonrandom with respect to egg size; larvae hatching from larger eggs survive better than larvae hatching from smaller eggs (Fox and Mousseau 1996). We thus examined the relationship between egg size and (1) survivorship and (2) growth of *S. limbatus* larvae. We also estimated the magnitude of selection on egg size on both *C. floridum* and *C. microphyllum* and on individual trees within each species. Both egg length and width are normally distributed so that parametric models are appropriate for measuring selection. Selection differentials (S) for egg length and width were calculated separately for each *C. floridum* and *C. microphyllum* tree within the population as the average size of an egg that successfully penetrated the seed coat minus the average size of all eggs laid on seeds of that tree (Falconer 1989). Selection differentials were converted to selection intensities (i), with $i = S/s$, where S is the selection differential and s is the standard deviation in egg size (Endler 1986). Selection intensities can be used to evaluate selection independently of the phenotypic mean and variance. Each family was treated as an independent data point; an average egg size was calculated for each mother and an average survivorship was calculated for her progeny.

An average of 7.3 families were reared on seeds of each of 10 *C. floridum* and 10 *C. microphyllum* plants (total = 73 families with an average of 11.9 progeny on *C. floridum*, and 73 families with an average of 13.0 progeny on *C. microphyllum*).

Seed coat resistance and selection on egg size in the field and laboratory

In this next study we (1) examined seed coat resistance and selection on egg size for multiple populations of trees in the field, and then (2) replicated the first experiments in the laboratory with trees for which we had field data to confirm that patterns observed in the laboratory were predictive of the patterns observed in nature.

In 1997 we collected seeds from >15 trees from each of four populations of *C. floridum* (Apache Junction population, along Mountainview Road in Apache Junction, Pinal County, Arizona, 10 to 14 August 1997; Scottsdale population, Scottsdale Highway, 1.7 miles north of Bell Road [behind the Scottsdale Well], in Scottsdale, Maricopa County, Arizona, 9 August 1997; Earp population, along Highway 62 and Old Parker Dam Road near Earp, San Bernadino County, California, 8 August 1997; and Glamis population, along Highway 78 on the Algodones Dunes near Glamis, Imperial County, California, 7 August 1997). The focus of this study is on seeds of *C. floridum*, but for comparative purposes seeds were also collected from >20 individual *C. microphyllum* trees at the Apache Junction population and from >20 individual *A. greggii* plants (shrubs) at the Earp population. Seeds of *C. microphyllum* were not collected from the Earp population because all plants at this site had abscised their fruits earlier in the season. *C. microphyllum* does not occur at the Glamis and Scottsdale sites. Also, to compare the size of eggs that have evolved in beetle populations with access to *C. floridum* to the size of eggs that has evolved in a population without access to *C. floridum,* we collected seeds from >10 *A. greggii* along Highway 60, near Wenden, La Paz County, Arizona (Wenden population). There are no *C. floridum* at this location, with the exception of a few ornamental plants.

In 1998 seeds were collected from two populations of *C. floridum*; from 27 trees in north Phoenix (Phoenix population) along Carefree Highway just east of the junction with I17, Maricopa County, Arizona, and from 54 trees in the Scottsdale population described earlier. Fruits were collected and handled exactly as in 1997 except that all seeds bearing eggs were kept separate for each tree. Seed coat resistance and selection on egg size were each quantified as in the previous experiments. For all analyses, each seed was treated as a single data point within each tree.

Enough fruits were collected from each tree to fill a 3.8-L (1 gallon) plastic bag or, if there were few fruits on a tree, all fruits were collected. Within 24 h of collection, fruits were separated into two categories: damaged and undamaged. Only damaged fruits are accessible for oviposition because female *S. limbatus* lay eggs directly onto seeds inside the fruit. Fruits were considered damaged if they had been partially eaten by rodents or had emergence holes of other insects in the fruit wall (holes large enough for *S. limbatus* females to enter). Damaged fruits were opened and seeds bearing beetle eggs were separated from those not bearing eggs. Eggs remain attached to seeds long after they have hatched and beetles have completed development and left the seed, allowing the fate of each egg to be determined. Undamaged fruits were shipped back to the laboratory for the experiment described below.

Seed coat resistance and selection on egg size in the field.—Eggs from the above collections were measured and scored for survivorship within 4 d of collecting. This ensured that all eggs scored were laid in the field and not in bags. Eggs were measured (length and width) using an ocular micrometer and scored for whether larvae successfully penetrated the seed coat. Eggs containing living larvae that had not yet penetrated the seed coat were not scored since they may have been laid in the bags after fruits were removed from the tree.

For all statistical analyses, each seed was treated as a single data point because multiple eggs on a single seed may have been laid by the same female. The intensity of selection on egg size was estimated as in the first laboratory study, except that each seed (rather than each family) was treated as an independent data point; the size of each egg and the survivorship of larvae hatching from these eggs were averaged across all eggs on a seed to produce a single data point for each seed. Unfortunately, seeds bearing eggs from the 1997 collection were pooled (within populations) before measurements were taken, so variation among trees within a population could not be examined. Thus, estimates of egg size, seed coat resistance, and selection intensity in the 1997 study are population-level variables. In 1998 seeds bearing eggs were not pooled allowing among-tree variation (within populations) to be examined.

Seed coat resistance, larval growth, and selection on egg size in the laboratory.—In the 1997 collections described above, undamaged fruits from each tree were kept in separate bags. This allowed us to examine variation among individual trees within each population in a laboratory experiment. We chose 12 *C. floridum* trees from each of the four populations (Apache Junction, Scottsdale, Earp, and Glamis) and reared families of beetles on these seeds as in the first experiment. For comparative purposes, and so that we had replication of our experiment, we used two populations of *S. limbatus*. The first population (Earp) was collected as described above (Experiment 1). The second population was collected on 10–14 August 1997 from seeds of *C. floridum* and *C. microphyllum* in numerous locations in Apache Junction, Pinal County, Arizona (Apache Junction population). These two populations are similar in host plant availability; both have access primarily to *C. floridum* (abundant), *C. microphyllum* (abundant), and *A. greggii* (less common). Both populations were maintained in the laboratory on seeds of *A. greggii* for four generations prior to the experiment, at 30°C, L:D 15:9.

S. limbatus families were created as in the first experiment. Unlike the first experiment, eggs were not reared to adult; we scored only seed coat resistance and measured the size of eggs laid by each female. This experiment was executed in two blocks (one month apart) so a block effect is included in the statistical analyses. For all analyses individual data points represent the average size of all eggs laid by a single female or the average survivorship of all larvae hatching from those eggs (i.e., one data point per egg-laying female rather than one data point per egg). Selection on egg size (selection intensity) was measured as in the first laboratory experiment.

An average of 8.6 females from each beetle population laid eggs on seeds of each of the 12 *C. floridum* plants from each of the four *C. floridum* populations (total = 825 *S. limbatus* families and 12 338 eggs).

Female oviposition decisions: preference for seeds of less resistant trees?

The objective of this last experiment was to determine whether female *S. limbatus* distinguish among seeds of individual trees when laying eggs, and whether females preferentially lay eggs on seeds from less resistant trees.

Within each population of trees examined in the previous laboratory experiment (Apache Junction, Glamis, Earp, and Scottsdale populations) we identified the three or four trees that produced the most resistant seeds and the three or four trees that produced the least resistant seeds. Each preference test consisted of a single virgin female beetle confined in a 35-mm petri dish with a single virgin male and eight seeds from both one high-resistance tree and one low-resistance tree. Half of the seeds in a dish were marked with a black permanent marker (a single black dot) so that they could be identified after females were removed; in half the dishes, the more resistant seeds were marked, while in the other half the less resistant seeds were marked. Marking had no detectable effect on female oviposition preferences. Dishes were shaken (to ensure a random distribution of seeds within the dish) prior to the introduction of beetles. Each female was allowed to oviposit until she laid at least eight eggs.

For each population of trees, all possible combinations of resistant vs. susceptible seeds were tested. Oviposition preference is defined separately for each tree as the proportion of eggs laid on seeds of that tree when tested against all combinations of alternate class of seeds (i.e., those from either less or more resistant trees). No between population tests were performed.

RESULTS

Seed coat resistance, beetle growth and survivorship, and selection on egg size: variation among trees within a population

Seed coats of *Cercidium floridum* were substantially more resistant than seed coats of *C. microphyllum* to penetration by *Stator limbatus* larvae; mortality of larvae while penetrating the seed coat averaged 0.37 ± 0.08 on *C. floridum* and only 0.07 ± 0.03 on *C. microphyllum*; Table 1A). Other life history characters also indicate that *C. microphyllum* is more suitable than *C. floridum* for growth and development of larval *S. limbatus*: egg-to-adult survivorship was higher, development time was faster, and final adult body mass was higher on *C. microphyllum* than on *C. floridum* (Table 1B).

There was substantial variation among individual trees within species in the resistance of their seeds to penetration (Fig. 1, Table 2A) and in their suitability for *S. limbatus* growth and development (Figs. 1 and 2, Table 2B). On *C. floridum*, survivorship within seeds, egg-to-adult survivorship, development time of male and female larvae, and final adult body mass of male progeny (not significant for female progeny) also varied among individual trees (Figs. 1 and 2, Table 2B). Likewise, survivorship within seeds, egg-to-adult survivorship, development time of male progeny, and body mass of female progeny varied among individual *C. microphyllum* trees (Figs. 1 and 2, Table 2B).

There was a weak negative relationship (among trees) between the resistance of seeds to penetration by *S. limbatus* larvae and the survivorship of larvae within the seed; i.e., larvae survived better inside seeds for which larval survivorship during seed coat penetration was highest (Fig. 1A vs. B; Spearman rank-sum correlations of -0.383 [$P > 0.05$] and -0.794 [$P < 0.01$] for *C. floridum* and *C. microphyllum*, respectively). There were no other consistent relationships observed between seed coat resistance and the suitability of seeds for *S. limbatus* growth (Figs. 1, 2, and 3 are sorted according to the resistance of each tree's seeds to penetration by *S. limbatus* larvae; i.e., sorted according to Fig. 1A). The high correlation between seed coat resistance to penetration and egg-to-adult survivorship observed for both hosts is not meaningful because egg-to-adult survivorship includes both survivorship while

TABLE 1. Average egg size and larval performance of *Stator limbatus* on seeds of 10 *Cercidium floridum* and 10 *C. microphyllum* trees occurring sympatrically in Earp, California, USA.

Variable	Mean ± 1 SE *Cercidium floridum*	Mean ± 1 SE *Cercidium microphyllum*	*P*
A) Resistance of seed coats to *S. limbatus* penetration (proportion)	0.37 ± 0.08	0.07 ± 0.03	<0.001
B) Suitability of seeds for *S. limbatus* development			
Survivorship of larvae (proportion)			
Within seed	0.76 ± 0.06	0.83 ± 0.03	0.756
Egg-to-adult	0.52 ± 0.08	0.78 ± 0.05	<0.001
Development time (d)			
Female progeny	28.0 ± 0.52	23.3 ± 0.17	<0.001
Male progeny	28.2 ± 0.54	23.5 ± 0.22	<0.001
Adult body mass (mg)			
Female progeny	3.17 ± 0.05	3.60 ± 0.05	<0.001
Male progeny	3.37 ± 0.07	3.81 ± 0.04	<0.001
C) Size of eggs laid by females (mm)			
Egg length	0.581 ± 0.004	0.550 ± 0.003	<0.001
Egg width	0.418 ± 0.003	0.390 ± 0.001	<0.001

Notes: Means were calculated first across siblings within families, then across families within individual trees, and then across trees within each host. Comparisons were made with a Mann-Whitney *U* test treating each tree as an individual data point. Note that the egg size differences reflect nearly a 30% increase (by volume) in the size of eggs laid on *C. floridum* relative to *C. microphyllum*. Seed coat resistance is defined as: 1 − survivorship of larvae during seed coat penetration.

penetrating the seed (which is just one minus seed coat resistance) and survivorship within the seed. For both species, seeds on which larval development time was long were the same seeds on which beetles emerged as small adults; Spearman rank-sum correlations between development time and body mass were −0.650 and −0.833 for male and female beetles reared on *C. floridum* ($P < 0.05$ for each) and −0.176 and −0.612 on *C. microphyllum* ($P > 0.05$ for each, probably due to small sample sizes).

When pooling data for all individual *C. floridum* trees, treating each beetle family as an independent data point (rather than each tree), we observe that larvae developing from large eggs were more likely to successfully penetrate seeds than larvae developing from small eggs (Table 3), consistent with previously published data (Fox and Mousseau 1996, Fox et al. 1997*a*, *b*). This indicates that larvae hatching from large eggs are less impacted by seed coat defenses than larvae hatching from small eggs. Both survivorship within the seed and egg-to-adult survivorship on *C. floridum* were also positively correlated with egg size (both egg length and egg width; Table 3), resulting in directional selection for large eggs on *C. floridum*, with an estimated selection intensity of $i = 0.228 \pm 0.101$ (for egg length). In contrast, there was only a marginally significant relationship between egg size and the ability of larvae to penetrate the seed coat of *C. microphyllum* seeds (Table 3; $P < 0.05$). There was no significant relationship between egg size and either survivorship of larvae within seeds or egg-to-adult survivorship on *C. microphyllum*, indicating little if any advantage to developing from a large egg when reared on this host. We thus found no evidence of directional selection on this host (selection intensity, $i = -0.017 \pm 0.215$ for egg length). Females also exhibited egg size plasticity in response to the two paloverde species; they laid larger eggs on seeds of *C. floridum* than on seeds of *C. microphyllum* (Table 1C, Fig. 3), consistent with the hypothesis of adaptive plasticity in response to differences in selection on egg size.

The relationship between egg size and larval survivorship varied among individual *C. floridum* trees within the Earp population; in an analysis of covariance there were significant egg size × individual tree interactions for seed coat resistance to penetration by *S. limbatus* and egg-to-adult survivorship of larvae ($P < 0.05$ for both egg length and egg width), although not for larval survivorship within *C. floridum* seeds ($P > 0.30$ for both egg length and egg width). The variation in the relationship between egg size and egg-to-adult survivorship translated into variation in selection intensities among trees, with *i* for egg length varying between −0.29 and 0.88. There was no evidence of a relationship between the magnitude of seed coat resistance and the magnitude of selection on egg size ($r = -0.25 \pm 0.59$). There was also no evidence that females responded to variation among trees by laying different sizes of eggs on seeds of the different individual *C. floridum* trees (Table 2, marginally significant

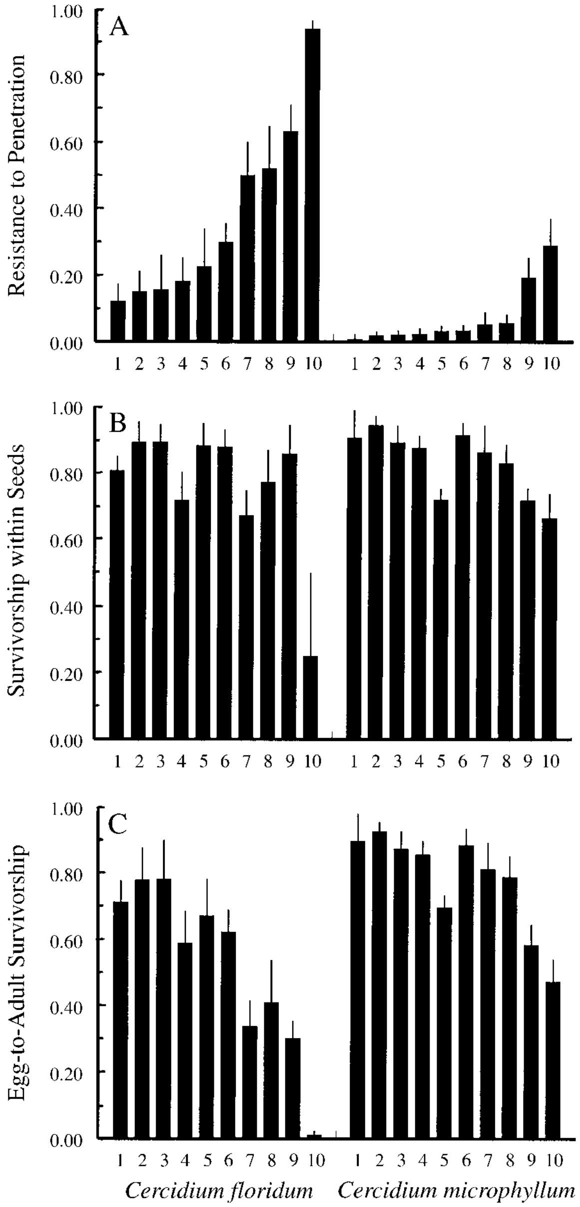

FIG. 1. Variation among individual *Cercidium floridum* and *C. microphyllum* trees in (A) the resistance of their seeds to penetration by *Stator limbatus* larvae, (B) survivorship of *S. limbatus* larvae within their seeds, and (C) egg-to-adult survivorship of *S. limbatus* larvae on their seeds. Trees in all panels are sorted according to their resistance to penetration to allow comparisons among panels. Statistics are in Table 2. All error bars are standard errors.

effect of individual tree on egg width, no significant effect on egg length; Fig. 3) and no evidence that females laid larger eggs on more resistant trees (Spearman rank-sum correlations >0.50 for both egg length and width).

There were no egg size × individual tree interactions for any character when larvae were reared on *C. microphyllum* and no variation among trees in the size of eggs laid by females (Table 2, Fig. 3).

Seed coat resistance and selection on egg size in the field and laboratory

Seed coat resistance and selection on egg size in the field.—In the 1997 field collection, the resistance of *Cercidium floridum* seeds to penetration by *S. limbatus* larvae varied substantially among tree populations (Mann-Whitney U test, $P = 0.009$). Trees from the Scottsdale site were the most resistant to larvae of *S. limbatus* (mean ± 1 SE across seeds = 0.41 ± 0.03, $N = 279$ seeds), trees from Apache Junction were intermediate (0.30 ± 0.06, $N = 39$ seeds) while trees from Earp were the least resistant (average across trees = 0.18 ± 0.06, $N = 23$ seeds) (field data were not collected from *C. floridum* at the Glamis site because beetle densities were very low). We also observed directional selection on egg size in the Scottsdale population (selection intensity, $i = 0.20$). However, we did not detect evidence of positive directional selection on egg size in either the Apache Junction or Earp populations ($i = 0.03$ and -0.06, respectively).

In the 1998 field collection, seeds of *C. floridum* trees varied significantly within populations in their resistance to penetration by *S. limbatus* larvae (this analysis was not possible for the 1997 collection). Seeds of trees at the Scottsdale site were slightly, but not significantly, less resistant to larval penetration (mean resistance, 0.33 ± 0.04, $N = 48$ trees) than seeds of trees at the Phoenix site (0.47 ± 0.08, $N = 19$ trees; Mann-Whitney U test, $P = 0.11$). Trees at the Scottsdale site were also slightly, but not significantly, less resistant than we had estimated at this site in 1997 (0.33 ± 0.04 in 1998 vs. 0.41 ± 0.03 in 1997; Mann-Whitney U test, $P = 0.09$). Directional selection favoring larger eggs at the Scottsdale site in 1998 was also substantially weaker (egg length, $i = 0.02 \pm 0.06$) than at the Phoenix site ($i = 0.20 \pm 0.06$; Mann-Whitney U test, $P = 0.02$), and lower than was observed at this site in 1997 ($i = 0.20$ in 1997; Mann-Whitney U test, $P < 0.01$).

At the Phoenix site there was a suggestion that the intensity of selection increased with increasing seed coat resistance (among trees, $r = 0.32$), but this correlation did not differ statistically from zero ($P = 0.18$). There was no evidence that the intensity of selection correlated with seed coat resistance at the Scottsdale site ($r = 0.02$, $P = 0.91$).

Females laid larger eggs on *C. floridum* in the field than on *C. microphyllum* (one-way ANOVA comparing the size of eggs laid on *C. floridum* vs. *C. microphyllum* in Apache Junction, the site where both hosts were collected; mean = 0.646 ± 0.005 mm and 0.624 ± 0.004 mm, respectively; $F_{1,117} = 11.18$, $P = 0.001$). Females also laid larger eggs on *C. floridum* than on *A. greggii*, as observed in previous laboratory experiments (one-way ANOVA comparing the size of eggs laid on *C. floridum* and A. *greggii* in Earp, the only

TABLE 2. One-way analyses of variance demonstrating variation among individual trees of *C. floridum* and *C. microphyllum* (within species) in the Earp population.

Variables	*Cercidium floridum*			*Cercidium microphyllum*		
	N	*P*	R^2	*N*	*P*	R^2
A) Seed resistance to *S. limbatus*	10	<0.001	0.58	10	<0.001	0.46
B) Seed suitability for *S. limbatus* development						
Survivorship of larvae						
Within seed	10	<0.001	0.38	10	0.003	0.31
Egg-to-adult	10	<0.001	0.51	10	<0.001	0.49
Development time (d)						
Female progeny	9	<0.001	0.45	10	0.062	0.23
Male progeny	10	<0.001	0.59	10	<0.001	0.37
Adult body mass (mg)						
Female progeny	9	0.194	0.19	10	0.05	0.23
Male progeny	10	0.024	0.34	10	0.39	0.14
C) Egg size of females (mm)						
Egg length	10	0.163	0.18	10	0.24	0.16
Egg width	10	0.066	0.21	10	0.90	0.06

Notes: Family means were used as data points for this analysis. *N*, number of trees.

site where both hosts were collected; mean = 0.654 ± 0.006 mm and 0.579 ± 0.006 mm, respectively; $F_{1,51} = 80.07$, $P < 0.001$).

The mean size of eggs laid on *C. floridum* varied among the tree populations (1997 data; one-way ANOVA, $F_{2,324} = 7.88$, $P < 0.001$). However, the variance among populations was actually small, with Scottsdale females laying the largest eggs (average egg length = 0.668 ± 0.002 mm), Earp intermediate (0.654 ± 0.006 mm), and Apache Junction smallest (0.646 ± 0.005 mm). Because seeds of *A. greggii* were collected from two sites, Earp (where *C. floridum, C. microphyllum*, and *A. greggii* are all sympatric) and Wenden (where only *A. greggii* occurs), we could also compare egg size among populations of beetles on this host. Because selection favors larger eggs on *C. floridum* than on *A. greggii* (Fox and Mousseau 1996), we expected Earp beetles to lay larger eggs on *A. greggii* than Wenden beetles (because there is no *C. floridum* at the Wenden site). However, the difference between populations was very small and not statistically significant (average egg length on *A. greggii*: Wenden 0.56 ± 0.00 mm, $N = 31$ seeds; Earp 0.58 ± 0.00 mm, $N = 30$ seeds; Mann-Whitney *U* test, $P = 0.08$).

Seed coat resistance and selection on egg size in the laboratory.—As in the field study, there was substantial variation in the laboratory study among individual *C. floridum* trees in the resistance of their seeds to penetration by *S. limbatus* larvae (Table 4, Fig. 4). Also, there was substantial variation among *C. floridum* populations in their average resistance to penetration by *S. limbatus* larvae (tree population effect in Table 4, Fig. 4). However, both populations of beetles examined (Apache Junction and Earp) performed similarly on all trees (i.e., there was no beetle population, beetle population × tree population, or beetle population × tree [within tree population] effect on larval survivorship during seed coat penetration; Table 4, Fig. 4).

As in the first laboratory experiment, both egg length and egg width were correlated with survivorship of larvae while penetrating the seed coat of *C. floridum*; larvae developing from larger eggs had higher survivorship during seed coat penetration than did larvae developing from small eggs (Table 5). This translated into directional selection favoring larger eggs in all four populations (Table 6). There was also a significant egg size × tree population effect (significant for both egg length and width) and an egg width × tree effect (within tree population; not significant for egg length) on larval survivorship during seed coat penetration (Table 5), as observed in the first experiment. These results demonstrate (1) that natural selection (via larval mortality) favors females that lay larger eggs because larvae hatching from larger eggs are better able to penetrate the seed coats of *C. floridum* seeds, and (2) that the magnitude of this natural selection varies among individual trees (within populations) and among populations of trees. Comparing among tree populations, selection intensity increased as tree resistance increased (ANCOVA, with beetle population as a factor and mean population resistance as a covariate; $F_{1,5} = 5.93$, $P = 0.06$ for the effect of tree resistance). This same pattern was observed within populations (across trees); the intensity of selection increased with increasing seed coat resistance in all of the beetle × tree combinations (Fig. 5, Table 6; least-squares regression, all analyses had positive slopes; $P < 0.05$ for four analyses, $P < 0.01$ for six of the analyses). The full analysis of covariance indicated that the intensity of selection (*i*) varied among tree populations ($F_{3,89} = 11.71$, $P < 0.001$) but not among beetle populations ($F_{1,89} = 1.96$, $P = 0.17$). The full ANCOVA also in-

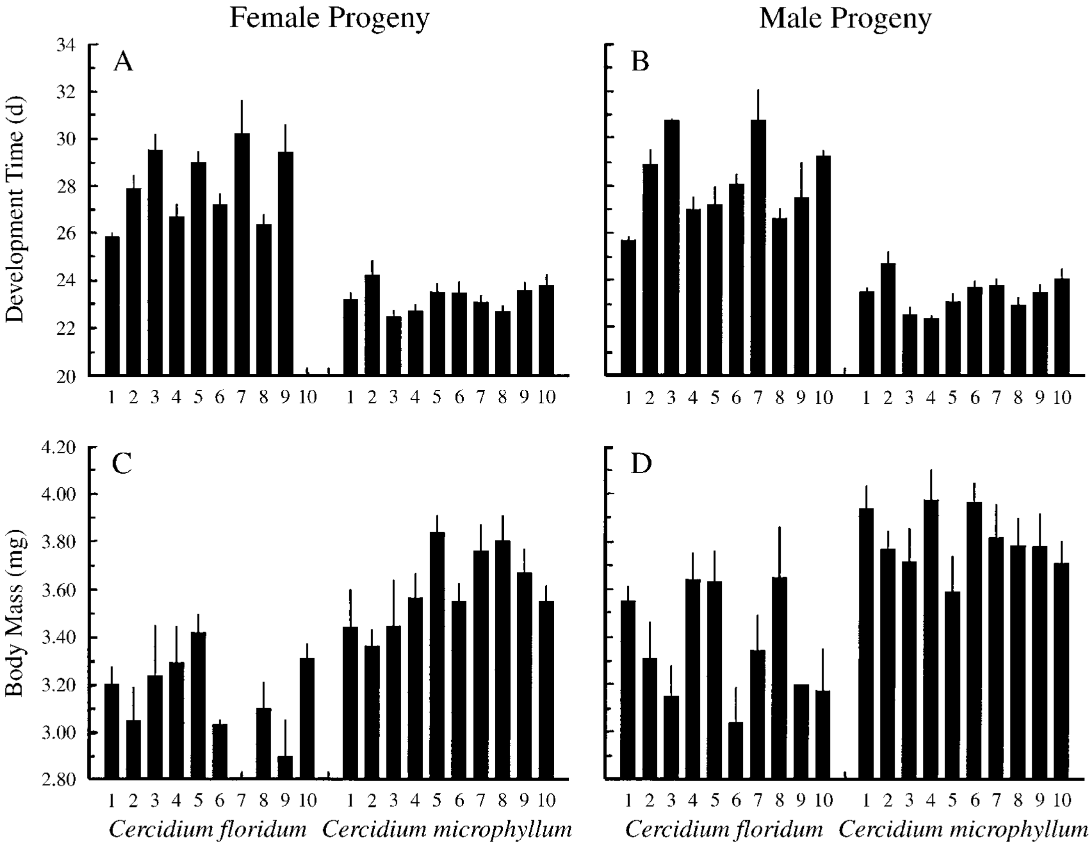

FIG. 2. Variation in the suitability of seeds from individual *Cercidium floridum* and *C. microphyllum* trees for the development of *Stator limbatus*. (A, B) Development time of beetles; (C, D) adult body mass of beetles at emergence. All panels are sorted (along the *x*-axis) in the same order as in Fig. 1A to allow comparisons between figures (i.e., trees are ranked according to the resistance of their seeds, from least to most resistant). Statistics are reported in Table 2. All error bars are standard errors.

dicated a highly significant relationship between seed coat resistance and the magnitude of selection on egg size ($F_{1,89} = 36.14$, $P < 0.001$).

Despite the demonstration that *C. floridum* trees vary substantially in the resistance of their seeds to penetration by *S. limbatus* larvae, there was no detectable variation among trees (within populations) or among populations of trees in the size of eggs laid by either the Earp or Apache Junction females (Table 4), indicating that females did not respond to variation in seed coat resistance by adjusting the size of egg that they laid.

Female oviposition decisions: preference for seeds of less resistant trees?

In paired preference tests, females preferentially oviposited on seeds of some trees over seeds of other trees (Fig. 6). However, there was no evidence that females preferred less resistant seeds; oviposition preference was not correlated with seed coat resistance in three of the four replicates (for Earp beetles on seeds of Earp, Apache Junction, or Scottsdale trees) and was opposite from the predicted pattern (i.e., females preferred to oviposit on the most resistant seeds) in the remaining replicate (Apache Junction beetles on seeds of Apache Junction trees).

DISCUSSION

Our first objective in this study was to quantify variation among individual *C. floridum* and *C. microphyllum* trees within populations, among populations, and between species in the resistance of their seeds to, and suitability of their seeds for development of *S. limbatus* larvae. As expected, we found substantial variation at all three levels. Seeds of *C. floridum* were a much poorer substrate for development of *S. limbatus* larvae than were seeds of C. *microphyllum*. However, individual plants varied substantially within populations of both species and among populations of *C. floridum*.

The two tree species also differed substantially in the average magnitude of selection imposed on seed beetle egg size; strong selection favored larger eggs when larvae were reared on seeds of *C. floridum*, but there was no selection on egg size when larvae were reared on *C. microphyllum*. Selection on egg size also

TABLE 3. The relationships between egg length and (A) resistance of *Cercidium floridum* and *C. microphyllum* seeds to penetration by *Stator limbatus* and (B) suitability of *C. floridum* and *C. microphyllum* seeds for larval *S. limbatus* development.

	Cercidium floridum		*Cercidium microphyllum*	
Variable	*N*	R^2	*N*	R^2
A) Resistance to penetration by *S. limbatus*	69	−0.211***	72	−0.057*
B) Suitability for *S. limbatus* development				
Survivorship				
Within seed	65	0.143**	72	+0.003$^{\mathrm{NS}}$
Egg-to-adult	69	0.298***	72	+0.011$^{\mathrm{NS}}$
Development time (d)				
Female progeny	57	−0.002$^{\mathrm{NS}}$	69	−0.059*
Male progeny	52	0.015$^{\mathrm{NS}}$	70	−0.097**
Adult body mass (mg)				
Female progeny	57	0.006$^{\mathrm{NS}}$	69	+0.027$^{\mathrm{NS}}$
Male progeny	52	0.000$^{\mathrm{NS}}$	70	+0.020$^{\mathrm{NS}}$

Notes: Results for egg width are similar. The sign on the R^2 value indicates the direction of the relationship. N = number of families. * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; NS, $P > 0.05$.

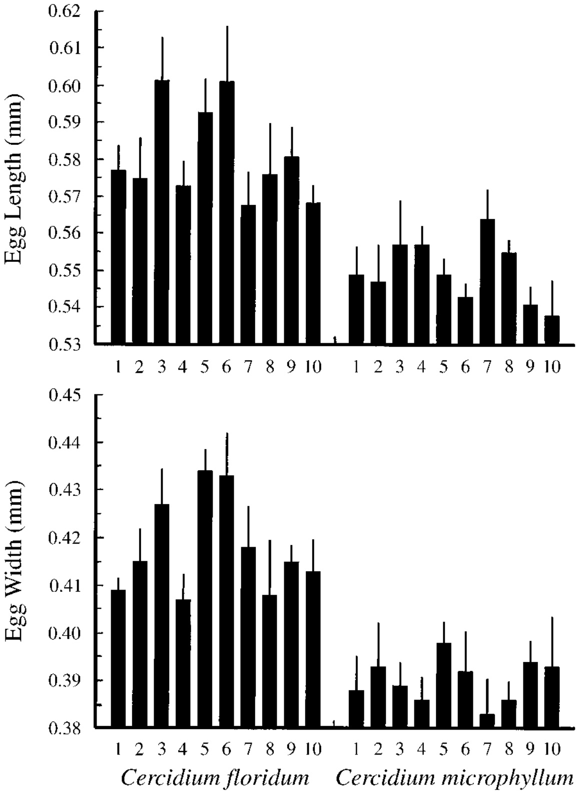

FIG. 3. Variation in the size of eggs laid by female *Stator limbatus* (egg length and width) among individual *Cercidium floridum* and *C. microphyllum* trees. Statistics are presented in Table 2. All error bars are standard errors.

varied substantially both among populations of *C. floridum* and among individual trees within populations. Selection intensities can vary across trees for two reasons (Endler 1986, Weis et al. 1992). First, the relationship between egg size and the fitness of progeny (the fitness function) may vary among trees. Alternatively, the phenotypic distribution in egg size may vary among trees (i.e., mean egg size varies among trees) due either to sampling error or differences in female responses to trees. The effect of sampling error on estimates of selection intensity is a possibility because the number of eggs sampled per tree (in the field) or the number of females laying eggs on each tree (in the laboratory) was small for some trees. However, there was no detectable variation among trees (within populations) in the size of eggs laid by beetles. Also, there was no evidence that selection intensities were correlated with mean egg size (among trees within a population). We thus conclude that selection intensities vary among trees because the relationship between egg size and larval survivorship varies among trees, and not due to sampling error or differences in female responses to trees.

TABLE 4. Analyses of variance demonstrating variation among tree populations and among individual trees of *Cercidium floridum* in seed coat resistance to *Stator limbatus*, but an absence of female *S. limbatus* responses to these seeds (as measured by egg size plasticity).

	Seed coat resistance			Egg length			Egg width		
Factor	df	*F*	*P*	df	*F*	*P*	df	*F*	*P*
Maternal mass	1	0.85	0.356	1	17.56	<0.001	1	25.04	<0.001
Experimental block	1	0.79	0.376	1	8.40	0.004	1	0.15	0.697
Beetle population	1	0.19	0.665	1	18.76	<0.001	1	3.71	0.054
Tree population	3	75.17	<0.001	3	1.93	0.124	3	2.05	0.105
Tree(tree pop.)	44	12.82	<0.001	44	1.30	0.096	44	0.97	0.527
Beetle pop. × tree pop.	3	0.42	0.738	3	1.76	0.152	3	2.11	0.098
Beetle pop. × tree(tree pop.)	44	0.81	0.812	44	0.96	0.549	44	0.80	0.801

Notes: This experiment was replicated across four tree populations (12 trees per population) and two beetle populations. ANOVAs were calculated using SAS GLM Type III sums of squares with maternal size (mass at adult emergence) as a covariate, tree (within tree population) treated as a random effect, and block, beetle population, and tree population treated as fixed effects. Note the large effects of tree population and tree (within tree population). All higher-order interactions were nonsignificant, and thus deleted from the model.

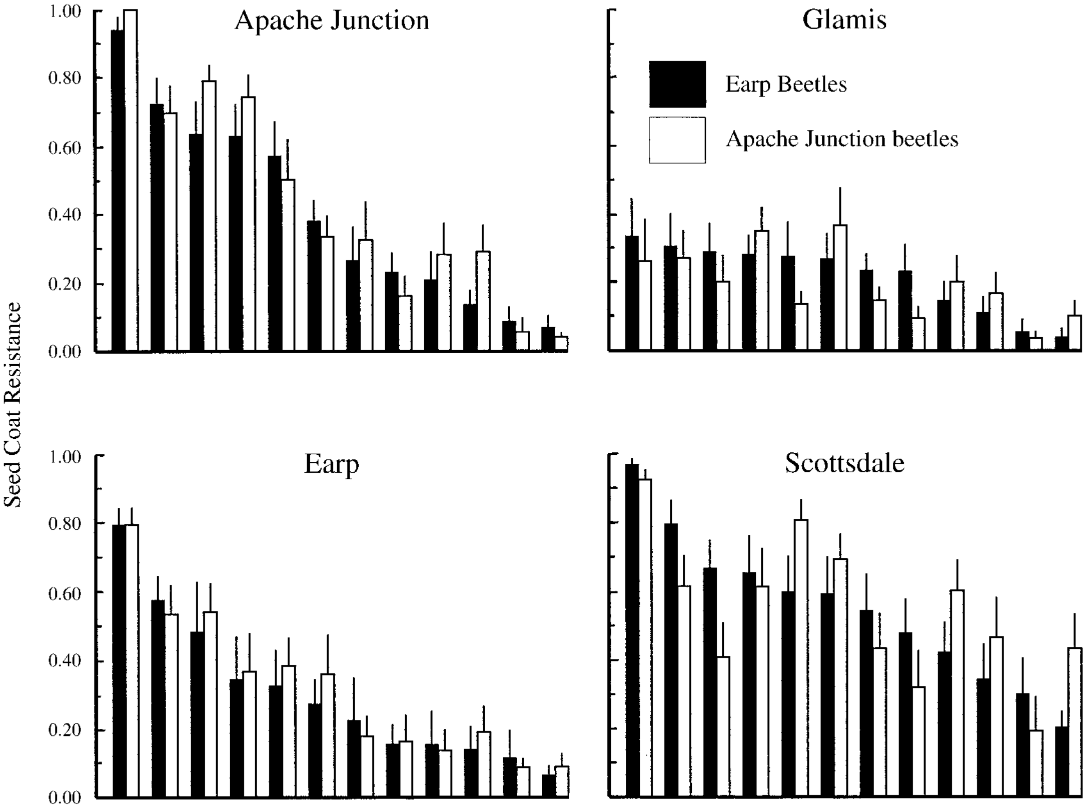

FIG. 4. Variation in the resistance of seed coats to penetration by *Stator limbatus* larvae among individual *Cercidium floridum* trees within tree populations, and among four populations. This experiment was replicated for two populations of *S. limbatus*. Means are presented in Table 6. All error bars are standard errors.

Selection intensities increased with increasing seed coat resistance, both among populations and among trees within populations. This is consistent with predictions of theoretical models, which generally predict that the magnitude of selection favoring large eggs should increase as environmental quality decreases (or as environmental stress increases) (Fox and Czesak 2000; e.g., Parker and Begon 1986, Sibly and Calow 1986). Few experimental tests of this prediction have been published, but those few are consistent with the prediction (e.g., Spight 1976, Ferguson and Fox 1984, Braby 1994, García-Barros 1994, Fox and Mousseau 1996, Einum and Fleming 1999, Fox 2000). However, with the exception of Fox (2000) these studies have examined few environments (generally only two or three) such that their generality is unclear. In this study we have examined variation in selection among 12 environments within each of four tree populations.

TABLE 5. Analyses of covariance examining the effects of egg size on ability of larval *Stator limbatus* to penetrate the seed coats of *Cercidium floridum* seeds.

	Egg length			Egg width		
Factor	df	*F*	*P*	df	*F*	*P*
Experimental block	1	0.00	0.990	1	0.44	0.508
Beetle population	1	3.41	0.065	1	0.67	0.414
Tree population	3	6.65	<**0.001**	3	6.35	<**0.001**
Tree(tree pop.)	44	1.15	0.240	44	1.43	**0.038**
Egg size	1	177.88	<**0.001**	1	237.12	<**0.001**
Egg size × tree pop.	3	5.42	<**0.001**	3	5.04	**0.002**
Egg size × tree(tree pop.)	44	1.14	0.256	44	1.43	**0.039**

Notes: ANCOVAs were calculated using SAS GLM Type III sums of squares with egg size as a covariate, tree (within tree population) treated as a random effect, and block, beetle population, and tree population treated as fixed effects. Values with probabilities in bold are statistically significant at $P < 0.05$. All higher-order interactions were nonsignificant, and thus deleted from the model.

TABLE 6. Mean seed resistance and selection on egg length (*i*, selection intensity) (± 1 SE) for two populations of *Stator limbatus* reared on seeds from four populations of *Cercidium floridum* trees.

	Beetle population			
	Apache Junction		Earp	
Tree population	Resistance	*i*	Resistance	*i*
Apache Junction	0.44 ± 0.09	0.40 ± 0.12	0.41 ± 0.08	0.54 ± 0.18
Glamis	0.20 ± 0.03	0.31 ± 0.11	0.22 ± 0.03	0.31 ± 0.07
Earp	0.32 ± 0.06	0.31 ± 0.14	0.31 ± 0.06	0.61 ± 0.11
Scottsdale	0.54 ± 0.06	0.98 ± 0.14	0.50 ± 0.05	0.59 ± 0.25

Notes: Data are from the laboratory second experiment. Selection intensities were calculated separately for each tree and then averaged across trees (12 trees per population). With each tree, each beetle family was treated as an independent data point.

Previous studies of selection on egg size in *S. limbatus* are consistent with our current results and with theoretical predictions. Fox and Mousseau (1996) demonstrated that the intensity of selection favoring large eggs is substantially greater on seeds of *C. floridum* (which produces relatively resistant seeds) than on seeds of *A. greggii* (which produces relatively susceptible seeds). We found the same result here for our comparison of *C. floridum* with *C. microphyllum*. Also, Fox (2000) demonstrated that selection increases with seed coat resistance in a comparison of individual *C. floridum* trees within a population. However, that study included only a single population. We have obtained that same result for four tree populations, with two beetle populations reared on each (second experiment; Fig. 5). Only one laboratory comparison presented here failed to find a positive relationship between seed coat resistance and selection intensity (for Earp trees in the first experiment). In that regression, the relationship between seed coat resistance and selection intensity was negative (although not significant statistically). We also observed high variation in our estimates of selection intensity in the field (both in 1997 and 1998) and only observed a positive correlation between selection

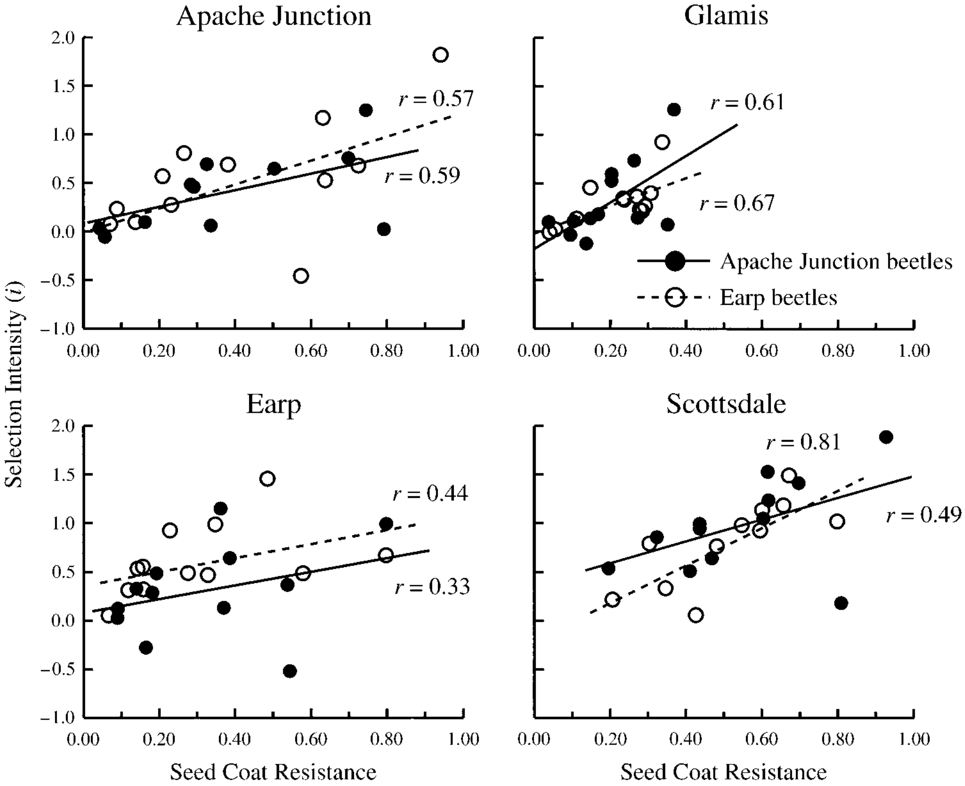

FIG. 5. The relationship between seed coat resistance and the magnitude of natural selection favoring large eggs (selection intensity, *i*) for two populations of *Stator limbatus* reared on seeds from four populations of *Cercidium floridum* trees. Each data point is the mean for a single tree within a population.

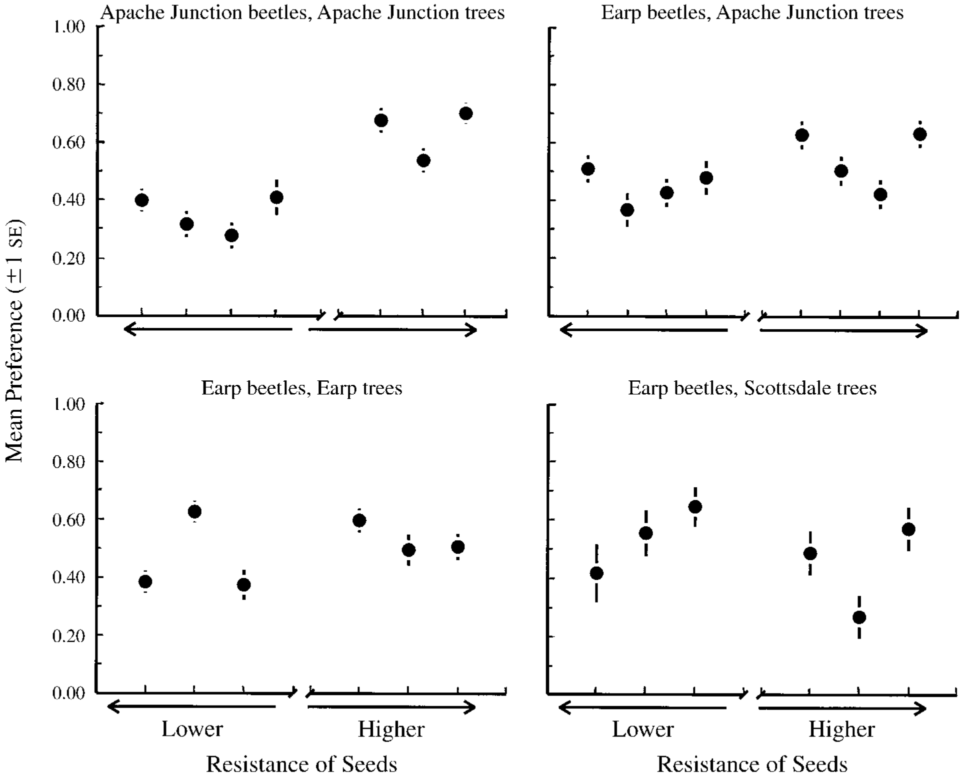

FIG. 6. Oviposition preference of *Stator limbatus* females for seeds of individual trees. Preference for seeds of each tree is defined as the proportion of a female's eggs laid on seeds of that tree in a paired preference assay. The *x*-axis is the rank order of larval mortality while penetrating seeds.

intensity and seed coat resistance in one of the two field samples for which such an estimate was possible (in 1998). It is unclear, however, if this variation among years and study sites reflects true variation rather than sampling error since sample sizes were generally small for the field studies and estimates of selection were much more variable in the field than in the laboratory (as also observed in Fox 2000).

Because trees vary substantially in both the resistance of their seeds and the suitability of their seeds for larval development, female beetles should experience selection favoring the ability to distinguish seeds from more suitable vs. less suitable trees. To test whether females had evolved this ability, we examined two responses of female *S. limbatus* toward seeds. First, we examined female life history responses to seeds of variable resistance. Previous research has demonstrated that *S. limbatus* females exhibit egg size plasticity in which they lay larger eggs on seeds of *C. floridum* than on seeds of the less-well defended *A. greggii* (Fox et al. 1997*a*). When comparing among species, we found the same result here; selection favors larger eggs on seeds of *C. floridum* than on *C. microphyllum*, and females responded by laying larger eggs on seeds of *C. floridum* than on *C. microphyllum*. We also found that selection on egg size varied substantially across individual trees, but found no evidence that females laid larger eggs on seeds of better defended trees within a species. This is consistent with previous data suggesting that the traits influencing seed resistance segregate independently from the cues used by females when adjusting egg size (Fox et al. 1997*b*).

Our second approach to testing whether females could distinguish more suitable from less suitable seeds was to use a paired preference test (Singer 1986). Although female *S. limbatus* clearly preferred to oviposit on seeds of some trees vs. seeds of other trees, we found no consistent relationship between female preference and tree resistance, a result commonly observed for herbivorous insects (Mackay 1985, Karban and Courtney 1987, Valladares and Lawton 1991, Larsson and Strong 1992, Zangerl and Berenbaum 1992, Underwood 1994). One possible explanation for the lack of a preference for less resistant seeds is that seed coat resistance is only one of the factors that influence offspring fitness, and the various components of offspring performance were not correlated among trees (Thompson 1988, Nylin and Janz 1993). A more likely explanation may be that our preference experiment is too artificial to quantify female behavior adequately. Seeds in a petri dish likely adequately reflect the experience a female encounters after entering a seed pod, and females correctly identify seed species when determining which size egg to lay, but oviposition preferences may be manifest before entering the seed pod (in response to fruit or vegetation). Our design examines female preferences at the level of the seed and not at the level of the fruit or tree.

Thus, we have demonstrated substantial variation in seed coat resistance to larval *S. limbatus* and suitability of seeds for the development of larvae between *Cercidium* species, among populations within species, and among individual trees within populations. This variation has a large influence on the magnitude of natural selection on seed beetle egg size, with selection favoring larger eggs on more resistant trees. Female beetles respond to the variation in selection among species (*C. floridum* vs. *C. microphyllum*) by adjusting their egg size; they lay larger eggs on the host upon which selection favors larger eggs, and lay smaller eggs on the host upon which selection does not favor larger eggs (and thus have higher fecundity; Fox et al. 1997*a*). However, females do not distinguish between seeds of more vs. less resistant trees within a population of trees. They should thus experience substantial variation in selection on egg size within populations, the consequences of which require further investigation.

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