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NATURAL SELECTION ON SEED-BEETLE EGG SIZE IN NATURE AND THE LABORATORY: VARIATION AMONG ENVIRONMENTS

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Abstract. The size of eggs that evolves within a population will in theory reflect a balance between selection for large eggs and for increased fecundity. Theory also predicts that the intensity of selection for large eggs (via effects of egg size on progeny survival and growth) increases as environmental quality decreases. I took advantage of variation in seed quality among individuals within one population of a single tree species, *Cercidium floridum*, to (1) quantify variation in the magnitude of selection on seed beetle (*Stator limbatus*) egg size, and (2) test the hypothesis that the intensity of selection on egg size increases with decreasing host plant quality. The proportion of larvae that failed to penetrate the seed coat varied substantially among individual trees and was used as a measure of seed-coat resistance. The intensities of selection (i) on egg size also varied among trees. This measure i was positively correlated (among trees) with the resistance of seed coats to penetration by larvae of *S. limbatus*, indicating that that selection is greatest on trees upon which larval survivorship was lowest. This study thus demonstrates that the intensity of selection on egg size increases as larval environmental quality decreases.

Key words: Cercidium; *natural selection; paloverde; seed-coat resistance; selection differentials; selection intensity;* Stator; *survivorship.*

Introduction

Egg size is a maternal character that can have a substantial influence on progeny fitness by determining starting resources and size (Sinervo 1991). Models of the evolution of progeny size (e.g., Smith and Fretwell 1974; reviews in Clutton-Brock 1991, Roff 1992, Stearns 1992) generally start with two assumptions; (1) progeny fitness increases with increasing parental investment per offspring, and (2) there is a trade-off between the number of progeny a female can make and the amount of resources allocated to each of them. Thus, the size of eggs that evolves in a population depends on a balance between selection for large eggs (because progeny hatching from larger eggs generally survive better, develop faster, or mature larger; review in Fox and Czesak 2000) and selection for small eggs (because females laying smaller eggs can have higher fecundity; Roff 1992, Stearns 1992, Bernardo 1996).

Simple models predict that as the relationship between progeny size and progeny fitness changes, the balance between selection for small eggs (through effects on fecundity) and for large eggs (due to effects on progeny fitness) will change, and thus optimal egg size will change (e.g., Smith and Fretwell 1974). The relationship between progeny size and fitness (and thus the magnitude of selection favoring large eggs) is expected to change as environmental conditions vary (review in Fox and Czesak 2000), and models generally predict that the magnitude of selection favoring large eggs should be greater in more adverse or lower quality environments (e.g., Parker and Begon 1986, Sibly and Calow 1986). Such variation in selection is often proposed as an explanation for geographic and seasonal variation in egg size (e.g., Fleming and Gross 1990, Beacham and Murray 1993, Rijnsdorp and Vingerhoed 1994, Azevedo et al. 1996; review in Fox and Czesak 2000). However, few studies have manipulated progeny environments and quantified the relationship between egg size and progeny growth or survival in each environment. These few studies have demonstrated that selection on egg size varies among environments (e.g., Richards and Myers 1980, Semlitsch and Gibbons 1990, McLain and Mallard 1991, Braby 1994, Carrière and Roff 1995, Fox and Mousseau 1996, Einum and Fleming 1999), and their results are generally consistent with the hypothesis that the intensity of selection for large eggs increases as environmental quality decreases (Spight 1976, Ferguson and Fox 1984, Braby 1994, García-Barros 1994, Williams 1994, Fox and Mousseau 1996). However, these experiments consider few environments (usually only two or three) and most are carried out in carefully controlled laboratory or greenhouse environments. Thus, the generality of these results, and their relevance to nature, are unclear.

The relationship between progeny size and fitness may also vary among progeny produced by a single female due to small-scale environmental variation. Theoretical models predict that increased variability in selection on progeny size will result in the evolution of larger progeny than predicted by models that assume

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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 (Capinera 1979, McGinley et al. 1987, Philippi and Seger 1989) or plasticity in progeny size (Clutton-Brock 1991, Roff 1992). However, few studies have examined variation in selection on egg size within populations (but see Nakasuji and Kimura 1984, Braby 1994, Fox and Mousseau 1996, Sinervo 1998).

In the seed beetle *Stator limbatus* (Coleoptera: Bruchidae), the relationship between progeny size and fitness varies among host-plant species (Fox and Mousseau 1996, 1998). When larvae are reared on seeds of blue paloverde tree, *Cercidium floridum* (Caesalpinioideae: Fabaceae), on which egg-to-adult survivorship is low (<50%), there is strong directional selection for large eggs (selection intensity $i = 0.25$–0.56; Fox and Mousseau 1996). There is weaker selection on egg size when larvae are reared on seeds of the small-leaf paloverde, *C. microphyllum* ($i \approx 0.05$; egg-to-adult survivorship >85%) and no selection on egg size when larvae are reared on seeds of catclaw acacia, *Acacia greggii* (Mimosoideae: Fabaceae; $i \approx 0$; egg-to-adult survivorship >95%) (Fox and Mousseau 1996, 1998). Thus, in laboratory studies the relative magnitude of selection for large egg size varies among these hosts in a manner consistent with the hypothesis that the intensity of selection on egg size increases with decreasing host quality.

Average egg-to-adult survivorship of *S. limbatus* is generally low on seeds of *C. floridum* (<50%) but individual trees vary substantially in their suitability, producing a spectrum from very poor quality (larval egg-to-adult survivorship near 0%) to very high quality environments (larval egg-to-adult survivorship near 100%). Here, I take advantage of this natural variation in seed quality to examine variability in selection within populations of *S. limbatus.* I have three objectives: (1) to quantify variation among conspecific host trees in the magnitude of selection on *S. limbatus* egg size in nature; (2) to test the hypothesis that the intensity of selection on egg size increases with decreasing host quality; and (3) to confirm that laboratory studies of selection on egg size accurately reflect processes observed in nature.

NATURAL HISTORY OF *STATOR LIMBATUS*

Stator limbatus is a generalist seed parasite distributed from northern South America to the southwestern United States (Johnson and Kingsolver 1976, Johnson et al. 1989, Nilsson and Johnson 1993). Throughout its large geographic range, it has been reared from seeds of >70 plant species in at least 9 genera. In the United States, and particularly in Arizona, *S. limbatus* is abundant on many species of *Acacia* and two species of *Cercidium* (*C. floridum* and *C. microphyllum*; paloverdes). Only one or a few hosts may be present at any single locality. Females oviposit directly onto host seeds (Mitchell 1977), and thus oviposition is restricted to seed pods that have either dehisced or been damaged by other organisms (such as rodents and other insects; McAuliffe [1990], Siemens et al. [1992]). Upon hatching, the larvae burrow into the seed, where they complete development and pupate. They emerge from seeds as adults, the only dispersing stage of this species. Larvae are restricted to the seed that their mother has chosen for them. Beetles require only the resources inside of a single seed to complete development. Seeds of both *C. floridum* and *C. microphyllum* are large enough to support the development of multiple larvae (Fox et al. 1996, Fox 1997).

Egg-to-adult survivorship on seeds of *C. floridum* is generally <50%. Most of this mortality (75–85%) occurs when first instars attempt to penetrate the seed coat (Fox et al. 1995), due at least in part to seed-coat defensive chemicals (Siemens et al. 1992). In a previous study (Fox and Mousseau 1996), we found most of the selection on egg length (intensity averaging $i = 0.37$) occurring during seed-coat penetration. Once inside the seed, larval mortality is low and selection on egg size is weak (Fox and Mousseau 1996, 1998). Thus, estimates of selection on egg size occurring during larval penetration of seed coats (mean $i = 0.37$, range = 0.21–0.52) are very similar to estimates of selection occurring between egg-laying and adult emergence (mean $i = 0.40$, range = 0.25–0.56). This previous study of selection on egg size pooled seeds across trees and thus did not consider individual trees as a source of variation.

Females glue their eggs to seeds, and these eggs remain attached after larvae enter the seed. Eggs laid in the field can thus be measured (length or width) and scored for whether larvae successfully penetrated the seed coat. Larvae that successfully penetrate the seed 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. 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.

METHODS

Natural selection on egg size in the field.—Mature fruits (seed pods) of *C. floridum* were collected between 8 and 16 August 1997, from 20 haphazardly selected trees in Scottsdale, Arizona (along Scottsdale Highway, north of Bell Road). Enough fruits were collected from each tree to fill a 3.8-L 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: those that were damaged and those that were not. Female *S. limbatus* lay eggs directly onto seeds inside of the fruit, so only damaged fruits are accessible for oviposition. 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 pass through). Damaged fruits were opened and seeds bearing beetle eggs were separated from those not bearing eggs. Undamaged fruits were shipped back to the laboratory. Seeds from each tree were kept separate.

All eggs were measured and scored for survivorship within 4 d of collecting fruits to ensure that all eggs scored had been laid in the field and not in bags. Eggs were measured (length and width) using an ocular micrometer. Egg length and egg width are both correlated with egg mass (egg length $r = 0.94$; egg width $r = 0.78$). Eggs were scored for whether the larva had successfully penetrated the seed coat. Mortality of *S. limbatus* larvae during seed-coat penetration, averaged across all seeds within each tree, is subsequently referred to as ''seed-coat resistance.'' Data were collected on 928 eggs laid in the field on seeds of 20 trees, with an average of 13.3 ± 6.2 seeds per tree and 3.5 ± 3.4 eggs per seed (means ± 1 SD).

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 for each *C. floridum* tree within the Scottsdale population. The selection differential was calculated 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). To allow these estimates of the magnitude of selection to be interpreted without reference to the phenotypic mean and variance of egg size, 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). Multiple eggs laid on a single seed may be laid by the same female, so 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.

I used linear regression (SAS Procedure GLM; SAS Institute 1985), to test the hypothesis that selection intensity (i) increases with increasing seed-coat resistance among the 20 trees.

Selection on egg size in the laboratory.—This experiment was designed to confirm that the among-tree variation in natural selection on egg size observed in nature could be duplicated in the laboratory where environmental experiences of egg-laying females and developing eggs can be controlled.

To establish a laboratory colony of *S. limbatus,* seeds were collected in August 1997 from fruits of >20 *Acacia greggii* trees along Highway 95 between Blythe and Earp, California, and along Highway 62 and Old Parker Dam Road near Earp, California (all sites are in San Bernardino County). This laboratory colony of *S. limbatus* was established with >300 individuals. The colony was reared in the laboratory for two generations at 29.5°–30.5°C, L:D 15:9 h, with a population size of continuously >200 individuals. Seeds of *A. greggii* were used to rear these beetles because mortality is low (<5%) on this host, minimizing selection prior to the experiment.

Seeds collected from 23 *C. floridum* trees in Scottsdale, Arizona, were used for this experiment. I used only seeds that were undamaged and had not been previously oviposited upon by *S. limbatus.* Nineteen of the 23 trees used in this experiment were the same trees used in the field study (one of trees examined in the field did not produce enough seed to be used in the laboratory experiment).

Mated pairs of *S. limbatus* were confined on seeds of one of the 23 *C. floridum* trees. Because females lay eggs directly onto seeds, seeds were removed from the bean (legume fruit) prior to the experiment. Mated pairs were created using virgin adults that had emerged within the previous 12 h. Pairs were confined in a 35-mm petri dish with 10 seeds from a single tree, and maintained in a reach-in growth chamber (29.5°–30.5°C, L: D 15:9). Each female was checked daily and removed when >10 eggs had been laid on the seeds. Egg size (length and width) was measured with an optical micrometer for two or three haphazardly chosen eggs per female.

After eggs hatched, larvae were allowed to develop for ~10 d and then scored for whether they penetrated the seed coat or not. In total, 3855 eggs were scored (seeds of 23 trees with an average of 11.0 ± 1.3 *S. limbatus* females per tree and 15.4 ± 5.3 eggs per female [means ± 1 SD]). The intensity of selection on egg size was estimated as for the field study, except that each family (rather than each seed) 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. Of the 23 trees, one was so resistant that only one larva successfully penetrated the seed coat. This tree was included in estimates of seed-coat resistance (for which $N = 91$ eggs from 5 females) but deleted from analyses of selection intensity (for which the sample size available to estimate the egg size of survivors was only $N = 1$ egg from 1 female).

I used linear regression (SAS Proc. GLM; SAS Institute 1985) to test the hypothesis that selection intensity (i) increases with increasing seed-coat resistance among the 22 trees.

RESULTS

Egg length and width are positively correlated with each other ($r = 0.66$ across females in the laboratory study), but egg length is better correlated with egg mass ($r = 0.94$) than is egg width ($r = 0.78$; Fox and Mousseau 1996). Thus, only results for egg length are presented. Results are qualitatively similar for both egg length and width (all results that are statistically significant for egg length are also significant for egg width).

In the field, 43 ± 5% of the seed coats (mean ± 1

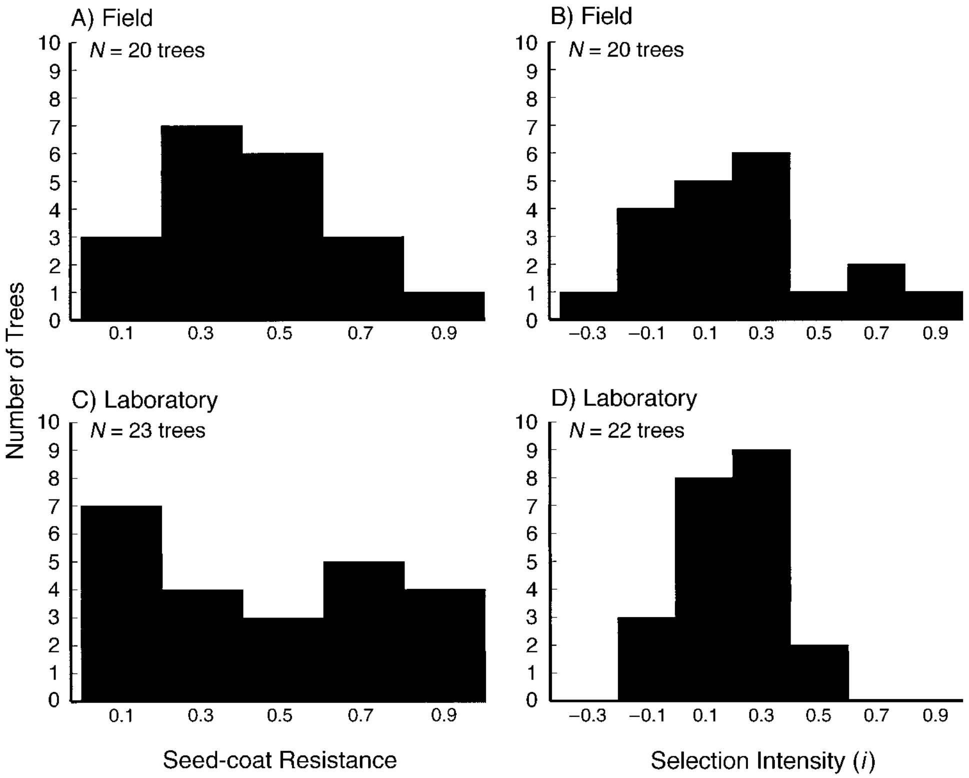

FIG. 1. Variation in the resistance of *Cercidium floridum* seed coats (A, C) and the intensity of selection on *Stator limbatus* egg length (B, D) among individual *C. floridum* trees in the field and the laboratory. Seed coat resistance is defined as the proportion of *S. limbatus* larvae that died while attempting to penetrate the *C. floridum* seed coat. For the field estimates of resistance, each seed was treated as a single independent data point within each tree. For the laboratory estimates, each beetle family was treated as a single independent data point within each tree. Scales on the *x*-axes show the midpoints of each interval.

SEM, $N = 20$ trees) resisted penetration by *S. limbatus* larvae. There was substantial variation among individual trees in the resistance of their seeds to larval penetration (Kruskal-Wallis analysis of variance, $\chi^2 = 61.6$, $P < 0.001$; $N = 20$ trees, with 13.3 ± 6.2 seeds per tree and 3.5 ± 3.4 eggs per seed [means ± 1 SD]), with resistance ranging from 0% to as high as 84% mortality (Fig. 1A). Resistance in the laboratory averaged 44 ± 7% for seeds of these same 19 trees and 48 ± 6% for the expanded sample of 23 trees (means ± 1 SEM). In the laboratory, as in the field, there was substantial variation among trees in the resistance of their seeds to larval penetration (Kruskal-Wallis analysis of variance, $\chi^2 = 266.8$, $P < 0.001$, $N = 23$ trees, with 11.0 ± 1.3 females per tree and 15.4 ± 5.3 eggs per female [means ± 1 SD]; resistance ranged from 3% to 99%; Fig. 1C). The estimates of seed-coat resistance of individual trees in the laboratory were positively correlated with the field estimates (Fig. 2; $r = 0.74$, $P < 0.001$).

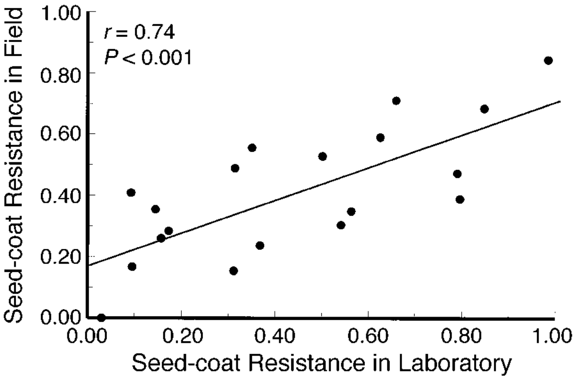

FIG. 2. The relationship between estimates of *Cercidium floridum* seed-coat resistance in the field and the laboratory. $N = 19$ trees.

The average intensity of selection on egg length across all trees was $i = 0.25 \pm 0.07$ in the field ($N = 20$ trees) and $i = 0.19 \pm 0.04$ in the laboratory ($N = 22$ trees) (means ± 1 SEM). This result indicates that eggs producing larvae that successfully penetrated the seed coat were on average 0.25 SDs (field) and 0.19 SDs (laboratory) longer than the mean size of all eggs laid. However, in both the laboratory and field there was substantial variation among trees in the intensity of selection on egg length (Fig. 1B, D), with *i* ranging from −0.25 to 0.82 in the field and from −0.26 to 0.56

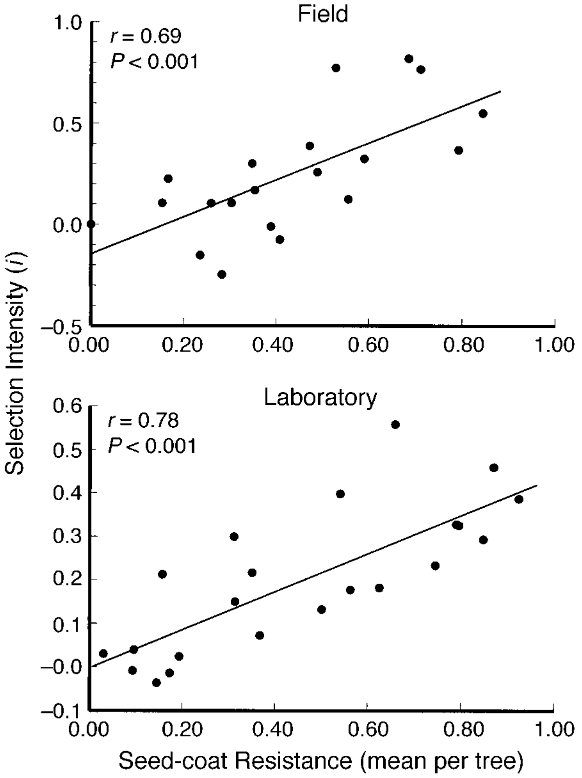

FIG. 3. The relationship between *Cercidium floridum* seed-coat resistance and the intensity of selection (*i*) on egg length in both the field and laboratory Each tree is treated as a single data point. $N = 20$ and 22 trees for the field and laboratory, respectively.

in the laboratory The estimates of *i* were positively correlated (among trees) between the field and laboratory ($r = 0.50$, $P = 0.03$), but were more variable among trees in the field than in the laboratory (Fig. 1B vs. 1D; $F_{18,18} = 2.73$, $P = 0.02$, for the 19 trees examined in both the field and the laboratory).

In both the field and the laboratory, the intensity of selection on egg size (*i*) was positively correlated (among trees) with the resistance of their seeds to penetration by *S. limbatus* larvae ($r = 0.69$ and 0.78, respectively, $P < 0.001$ for each); selection was greatest on seeds of trees upon which larval mortality was highest (Fig. 3). Selection intensity was not correlated with the mean size of eggs laid on seeds ($r = 0.20$ and 0.14, $P = 0.41$ and 0.53 for the field and laboratory, respectively).

DISCUSSION

The average intensity of selection on *Stator limbatus* egg size (across all trees of *Cercidium floridum*) was positive. However, the intensity of selection varied substantially among individual trees. Selection can vary across trees for two reasons; either the phenotypic distribution in egg size varies among trees (females may lay larger eggs on some trees) or the relationship between egg size and the fitness of progeny (the fitness function) varies among trees (Endler 1986, Weis et al. 1992). Because the number of eggs measured per tree was sometimes small, sampling error could produce variation among trees in measured egg size and thus indirectly influence estimates of selection intensity. However, selection intensity was not correlated significantly (among trees) with the mean size of eggs laid on seeds, indicating that among-tree variation in egg size does not explain the variation in selection. These results thus suggest that selection varies among trees because the relationship between egg size and larval survivorship varies among trees; as tree resistance increases (i.e., larval mortality increases), selection on egg size also increases. Unfortunately, although I present enough data per tree to calculate selection intensities for each tree, I do not have enough data to estimate the shape of the relationship between egg size and larval survivorship separately for each tree nor to test for variation among trees in this relationship.

Many theoretical models predict that the intensity of selection favoring large eggs will increase as environmental quality decreases (e.g., Parker and Begon 1986, Sibly and Calow 1986). My results support this hypothesis. Evidence from other organisms also supports this hypothesis. For example, many of the studies that have examined larval growth and development under adverse conditions have demonstrated that progeny hatching from larger eggs survive better, develop faster, or attain a larger adult size. In contrast, studies examining larval growth and development in benign/high-quality environments are frequently unable to detect an advantage to progeny of developing from large eggs (review in Fox and Czesak 2000). Results of comparative studies (among species or among populations within species) are also generally consistent with the hypothesis (e.g., Nakasuji 1987), but variation in egg size among species or populations can be confounded with other life history characters that coevolve with egg size (review in Fox and Czesak 2000). Experimental tests of the hypothesis have been performed only a few times. These studies manipulate larval environments and examine the effects on the relationship between egg size and some progeny character presumably correlated with fitness (e.g., survivorship, development time, body size at maturation). Results of these manipulations are mostly consistent with the hypothesis (e.g., Braby 1994, Fox and Mousseau 1996; but see Semlitsch and Gibbons 1990): the fitness advantages of hatching from a large egg generally increase with decreasing environmental quality. However, (1) these experiments often consider few environments, usually only two or three (e.g., Fox and Mousseau 1996, 1998); (2) egg size is often confounded with other variables (e.g., maternal age [Semlitsch and Gibbons 1990]) or generation within a season (Nakasuji and Kimura 1984); (3) the environments studied often differ in suites of variables that make identifying quality difficult (e.g., host plants can differ in many traits that can independently affect host quality and selection on egg size, resulting in a correspondence between host quality and selection intensity that does not necessarily reflect cause and effect [Braby 1994, Fox and Mousseau 1996, 1998]); and (4) most studies are carried out in carefully controlled laboratory or greenhouse environments. Thus, the generality of results of these manipulative experiments is unclear.

In the current study I have circumvented many of these problems. First, selection intensity was estimated in both the field and the laboratory, allowing results from a manipulative laboratory study to be compared to results from an unmanipulated comparative field study. Second, because each individual *C. floridum* tree represents a different selective environment, 20 (field) and 23 (laboratory) different environments could be examined, rather than just two or three. Third, quantifying environmental quality is straightforward because environments are defined according to their average effect on larval survivorship: trees on which larval survivorship is poor are clearly lower quality hosts than trees on which larval survivorship is high. Fourth, selection on egg size was examined in this study within a single population of a single insect species reared on seeds of a single host-plant species. Thus, life history traits that covary with egg size among insect populations or species, or that covary with environmental quality among beetle populations or host species, do not confound the relationship between egg size and selection intensity. Fifth, this study examines natural variation in egg size among females within a generation, rather than variation among seasons or variation in egg size due to maternal age, such that other life history variables that vary with maternal age or across seasons do not confound these results. This study is thus one of the few to demonstrate convincingly that the intensity of selection on egg size increases with decreasing environmental quality.

Although the current study demonstrates directional selection on egg size in the field, it does not demonstrate that egg size is evolving in *S. limbatus* populations. Even though egg size is heritable in *S. limbatus* (Fox et al. 1999), egg size probably changes little across generations in nature because of simultaneous directional selection for high fecundity and a trade-off between egg size and number (Fox et al. 1997). The current study considers only selection on egg size occurring during larval growth. Because adult *S. limbatus* feed little as adults, the trade-off between egg size and number is substantial and easily demonstrated (Fox et al. 1997). If this trade-off is similar in magnitude among populations of *S. limbatus*, and does not vary with environmental quality, my results indicate that the optimal *S. limbatus* egg size will vary among populations of *C. floridum*, with female beetles evolving to lay larger eggs in beetle populations that use more resistant trees. This prediction has not been tested. A similar result has already been obtained when comparing three of *S. limbatus*' host species; there is intense selection for large egg size when eggs are laid on *C. floridum* (on which larval mortality is very high, generally >50%), there is no detectable selection for large eggs when larvae are reared on *A. greggii* (on which larval mortality is very low, generally <5%), and the intensity of selection on egg size is intermediate between these extremes when larvae are reared on seeds of *C. microphyllum* (on which larval mortality is intermediate). Field and laboratory studies show that populations largely restricted to different hosts have evolved different egg sizes as predicted by the observed differences in selection on each of these hosts (Fox and Mousseau 1996; C. W. Fox and T. A. Mosseau, *unpublished data*).

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