

Egg-size manipulations in the seed beetle *Stator limbatus*: consequences for progeny growth¹

Charles W. Fox

Abstract: Studies that have demonstrated consequences of variation in egg size for progeny growth and development are often confounded by genetic correlations among life-history characters; relationships between egg size and progeny life-history characters do not always reflect cause and effect. Thus, experimental approaches to manipulating egg size in order to quantify the consequences of egg-size variation for progeny growth and development have been developed. I used egg-size plasticity in response to oviposition environment to manipulate egg size in a seed beetle, *Stator limbatus*, to test the hypothesis that progeny developing from larger eggs survive better, develop faster, and attain a larger adult body size than progeny developing from smaller eggs. Females exposed to *Cercidium floridum* during egg maturation laid eggs that were substantially larger than those laid by females exposed to *Acacia greggii* during egg maturation. The larger eggs laid by females exposed to *C. floridum* took significantly longer to hatch but had shorter total egg-to-adult development times than eggs laid by females exposed to *A. greggii* (when reared to adulthood on *A. greggii*). There was no evidence from the between-treatment comparisons that egg size affected egg-to-adult survivorship or the size at which progeny emerged as adults. Within-treatment correlations between egg size and progeny life-history characters were generally consistent with the between-treatment analyses, except that female progeny developing from larger eggs tended to emerge as larger adults than female progeny developing from smaller eggs. This result is interpreted as a consequence of heritable variation in body size rather than a cause-and-effect relationship between egg size and progeny body size.

Résumé : Les travaux qui ont démontré les conséquences de la variation de la taille des oeufs sur la croissance et le développement de la progéniture ont souvent ignoré les corrélations génétiques entre les diverses variables démographiques; les relations entre la taille des oeufs et ces variables ne sont pas toujours des relations de cause à effet. Des approches expérimentales ont été conçues pour manipuler la taille des oeufs dans le but de quantifier les conséquences de la variation de la taille des oeufs sur la croissance et le développement de la progéniture. J'ai misé sur la plasticité de la taille des oeufs en réaction aux conditions de la ponte pour manipuler cette variable chez un coléoptère des grains, *Stator limbatus*, et pour éprouver l'hypothèse selon laquelle la progéniture issue d'oeufs plus gros a une meilleure survie, un développement plus rapide et une taille adulte plus grande que la progéniture issue d'oeufs plus petits. Les femelles exposées à *Cercidium floridum* au cours de la maturation des oeufs ont pondu des oeufs beaucoup plus gros que ceux des femelles exposées à *Acacia greggii*. Les oeufs plus gros pondus par les femelles exposées à *C. floridum* ont mis significativement plus de temps à éclore, mais la durée de leur développement entre le stade oeuf et le stade adulte a été plus courte que celle du développement des oeufs des femelles exposées à *A. greggii* (larves élevées sur *A. greggii* jusqu'au stade adulte). La comparaison entre les deux traitements n'a pas permis de déterminer si la taille des oeufs affecte la survie au cours du cycle larve—adulte ou d'établir la taille de la progéniture au moment de la transformation en adulte. Les corrélations entre la taille des oeufs et les caractéristiques démographiques chez les insectes exposés à un même traitement sont généralement les mêmes que celles établies par comparaison entre deux traitements, sauf que la progéniture femelle issue des oeufs plus gros donne des adultes plus gros que ceux de la progéniture femelle issue d'oeufs plus petits. Il faut sans doute voir là la conséquence de la variation héréditaire de la taille du corps plutôt qu'une relation de cause à effet entre la taille des oeufs et la taille corporelle de la progéniture. [Traduit par la Rédaction]

Introduction

Egg size is an important life-history trait because it is simultaneously a maternal and an offspring character (Sinervo 1991). Thus, the amount of resources packaged in eggs can

affect both maternal and offspring fitness, causing an evolutionary conflict between a mother and her offspring. Theoretical examinations of egg-size evolution incorporate this parent—offspring conflict into models by assuming that offspring fitness increases as a function of egg size (Smith and Fretwell 1974; review in Bernardo 1996), and that there is a trade-off between egg size and maternal fecundity (i.e., producing larger propagules reduces fecundity). However, the generality of these assumptions is still unclear (review in Bernardo 1996; Kaplan 1998).

Egg size generally varies substantially within and among populations. Among populations this variation often covaries with measurable environmental variables and is therefore

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Charles W. Fox. The Louis Calder Center and The Department of Biological Sciences, Fordham University, 53 Whipoorwill Road, Box K, Armonk, NY 10504, U.S.A. (e-mail: fox@murray.fordham.edu).

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often interpreted as evidence of selection for larger eggs in more adverse environments (e.g., Fleming and Gross 1990). Consistent with this is the observation that under adverse conditions (such as during larval competition, periods of starvation, desiccation, or when larvae feed on low-quality resources), progeny hatching from large eggs generally survive better, develop faster, and attain a larger adult body size than progeny hatching from smaller eggs (e.g., Solbreck et al. 1989; Carlberg 1991; Tauber et al. 1991; Sota and Mogi 1992; Braby 1994; Fox and Mousseau 1996). However, for populations in more benign environments, such as low-density laboratory populations, the advantages of developing from larger eggs are often undetectable (e.g., Richards and Myers 1980; Wiklund and Persson 1983; Steinwascher 1984; Karlsson and Wiklund 1984, 1985; Wiklund and Karlsson 1984; Fox 1993). The results of the few studies that have successfully demonstrated consequences of natural variation in egg size (within populations) on progeny growth and development (reviewed for insects in Fox and Mousseau 1996) are often confounded by genetic correlations among life-history characters; relationships between egg size and progeny life-history characters do not always reflect cause and effect (Bernardo 1991; Fox 1994a, 1994b). Instead, because (i) most life-history characters are heritable (Mousseau and Roff 1987; Roff and Mousseau 1987), (ii) these characters are often correlated with body size, and (iii) maternal body size is generally correlated with egg size (review in Fox 1993; Heath and Blouw 1998), observed correlations between egg size and progeny phenotypes may frequently reflect a simple combination of genetic and environmental correlations between a mother and her offspring (e.g., large mothers lay large eggs, large mothers produce large progeny, and thus large eggs produce large progeny).

To examine the effect of egg size on offspring phenotypes independently of genetic correlations, experimental approaches to manipulating egg size directly have been developed (Sinervo and McEdward 1988; Sinervo 1990, 1993; Sinervo and Huey 1990; Sinervo and Licht 1991a, 1991b). These manipulations have demonstrated that egg-size variation has important consequences for progeny growth and development. However, while these manipulations have been very successful at elucidating patterns of selection on egg size in vertebrates, such techniques have not been readily applicable to invertebrates, in part because of the generally small size of their eggs. In this paper, I take advantage of natural plasticity in egg size in a seed beetle, *Stator limbatus* (Coleoptera: Bruchidae), to test the hypothesis that progeny developing from larger eggs survive better, develop faster, and attain a larger adult body size than progeny developing from smaller eggs when reared on seeds of a relatively high-quality host plant, *Acacia greggii* (on which egg-to-adult survivorship is very high).

Ecology of egg size in *S. limbatus*

Stator limbatus is a generalist seed parasite distributed from northern South America to the southwestern United States (Johnson 1963; Johnson and Kingsolver 1976; Johnson et al. 1989; Nilsson and Johnson 1993). Throughout its large geographic range, *S. limbatus* has been reared from seeds of >50 plant species in at least 9 genera. In the United States, particularly Arizona, it is abundant on many species of

Acacia (Fabaceae: Mimosoideae) and two species of *Cercidium* (*C. floridum* and *C. microphyllum*; palo verdes; Fabaceae: Caesalpinioideae), although only one or a few hosts may be available in any single locality. *Stator limbatus* oviposits directly onto host seeds and is thus restricted to seed pods that have either dehisced or 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 host seed their mother has chosen for them. Beetles require only a single seed to complete development and reproduce.

Selection on egg size varies substantially among the host plants of *S. limbatus*. For example, when larvae are reared on *C. floridum*, only larvae hatching from large eggs can penetrate the seed coat, selecting for progeny developing from large eggs (Fox and Mousseau 1996). In contrast, when larvae are reared on *A. greggii*, larvae hatching from small eggs penetrate the seed coat just as well as those hatching from large eggs, resulting in relaxed selection on egg size (egg-to-adult survivorship is generally >95% on this host). In fact, previous experiments have revealed no evidence of selection on egg size when *S. limbatus* larvae are reared on *A. greggii* (Fox and Mousseau 1996).

In response to this variation in seed quality, female *S. limbatus* have evolved egg-size plasticity: individual females vary the size of the eggs they lay according to the host that they lay on, laying substantially larger eggs on *C. floridum* than on *A. greggii*, but substantially more eggs on *A. greggii* than on *C. floridum* (because of a trade-off between egg size and egg number; Fox et al. 1997; Fox and Mousseau 1998). I made use of this plasticity to test the hypothesis that egg-size variation affects the growth and survival of larval *S. limbatus* reared on *A. greggii*.

Materials and methods

Study populations

Beetles for this experiment were collected from two localities in the southwestern United States. On July 3, 1995, beetles were collected from *C. floridum* and *C. microphyllum* in sandy washes along Parker Dam Road near Earp, California (Earp population). On August 20, 1995, beetles were collected from *C. floridum* and *C. microphyllum* from numerous locations in Apache Junction, Arizona (Apache Junction population). These two populations are >260 km apart, and acceptable host plants are distributed throughout the intervening region. Beetles and seed stock were both collected by picking mature seed pods from >25 host plants from each population. Mature pods were transferred to the laboratory and seeds containing beetles were separated from uninfested seeds. Seeds containing entrance or emergence holes of other bruchids (such as *Mimosestes* spp.) were discarded. Both laboratory populations were initiated with >300 field-collected individuals. Prior to this study, each population was reared in the laboratory on *A. greggii* (a natural host for *S. limbatus* in Arizona and California) for \approx 10 generations at 29°C and 15 h light (L) : 9 h dark (D) or 16 h L : 8 h D.

Egg-size manipulation

To test the hypothesis that egg-size variation affects the life history of progeny reared on *A. greggii*, I manipulated egg size by first exposing female *S. limbatus* to seeds of either *A. greggii* or *C. floridum* and then forcing all females to lay eggs on *A. greggii* (see

below). When females are first exposed to *C. floridum* (during egg maturation), they begin laying eggs that are $\approx 40\text{--}50\%$ larger (by mass) than those of females exposed to *A. greggii* during egg maturation (Fox et al. 1997; Fox and Mousseau 1998). This difference in egg size between *A. greggii*- and *C. floridum*-exposed females persists for $\approx 24\text{--}36$ h after females are switched to a different host plant (from *C. floridum* to *A. greggii* or vice versa; Fox et al. 1997). Thus, I conditioned females to lay either large or small eggs and then forced them to lay for 24 h on *A. greggii*, on which their progeny were reared to adulthood.

Virgin males and females were collected from isolated seeds of *A. greggii* (the host on which colonies were reared in the laboratory) within 12 h of adult emergence. Each beetle was weighed and then paired with a single virgin beetle of the opposite sex. Pairs were confined in a 35-mm petri dish containing 12 seeds of either *A. greggii* or *C. floridum*. Dishes were checked for eggs every 12 h until the female laid at least one egg. Females were then switched to a dish containing 15 seeds of *A. greggii* and allowed to lay eggs. After 12 h, dishes were examined and all seeds bearing eggs were removed and replaced with clean seeds; females were then allowed to lay for another 12 h.

All progeny were reared to adulthood at a density of one beetle per seed (excess eggs were scraped from the seed) at 29°C and 16 h L : 8 h D. Egg-to-adult development time (± 12 h; including embryonic, larval, and pupal stages), body mass at emergence, and egg-to-adult survivorship were recorded for each beetle. The size of eggs laid on *A. greggii* was recorded for each female by measuring 3 haphazardly selected eggs with an optical micrometer on a $50\times$ dissecting scope. Based on egg dimensions (length and width), egg mass was estimated as follows: egg mass = $-0.035 + 0.0086 \times$ egg length + $0.0022 \times$ egg width (Fox and Mousseau 1996). The data on egg mass given throughout this paper are qualitatively identical with those obtained in separate analyses of egg length and width.

Because the above experiment estimated only egg-to-adult development time (including embryonic, larval, and pupal development times), a second experiment was executed to test the hypothesis that embryos developing inside large eggs take longer to hatch than embryos developing inside small eggs. As in the above experiment, virgin males and females were collected from isolated seeds of *A. greggii* within 12 h of adult emergence, and pairs were confined in a 35-mm petri dish containing 12 seeds of either *A. greggii* or *C. floridum*. Dishes were checked for eggs every 12 h until the female laid at least one egg. Females were then switched to a dish containing 8 seeds of *A. greggii* and allowed to oviposit for 8 h. All eggs laid during this time were checked at 8-h intervals until they hatched. Egg hatch was defined as the time at which the larva developing inside the egg began to dig into the seed. Larval digging is easily scored under a dissecting scope because of a rapid buildup of frass inside the egg. It was not possible to estimate also the time at which larvae completely penetrated a seed because the rapid accumulation of frass in the egg obscured the movements of larvae and their entrance holes.

Both replicates of the experiment (Apache Junction and Earp populations) were executed simultaneously within a single environmental chamber. Dishes from each population and each treatment were interspersed randomly and rotated regularly to control for environmental gradients within the chamber.

Results

In both populations of *S. limbatus*, females first exposed to *C. floridum* (subsequently referred to as *C. floridum*-conditioned females) laid eggs that were substantially larger (by $\approx 25\%$) than eggs laid by females first exposed to *A. greggii* (*A. greggii*-conditioned females) (Fig. 1; estimated egg mass (mean \pm SEM) followed by the number of

families and the conditioning host in parentheses: Apache Junction, 0.0235 ± 0.0003 mg (32; *C. floridum*) and 0.0190 ± 0.0003 mg (32; *A. greggii*); Earp, 0.0256 ± 0.0003 mg (39; *C. floridum*) and 0.0203 ± 0.0002 mg (42; *A. greggii*). The larger eggs laid by *C. floridum*-conditioned females took significantly longer to hatch than the smaller eggs laid by *A. greggii*-conditioned females (86.8 ± 0.8 vs. 79.0 ± 0.5 h, $N = 16$ families each; one-way analysis of variance, treatment effect, $F = 151.6$, $P < 0.001$; family (treatment) effect, $F = 10.5$, $P < 0.001$).

Despite taking ≈ 8 h longer to hatch, progeny hatching from eggs laid by *C. floridum*-conditioned females emerged as adults significantly sooner (i.e., had shorter egg-to-adult development times) than progeny hatching from eggs laid by *A. greggii*-conditioned females (Fig. 2, Table 1). However, this treatment effect on development time was fairly small (<0.6 d) for each sex in each population, and treatment accounted for $<7\%$ of the variance in overall development time for each sex (estimated using the restricted maximum likelihood method of PROC VARCOMP of SAS (SAS Institute Inc. 1985), assuming population, family, and treatment were each random effects).

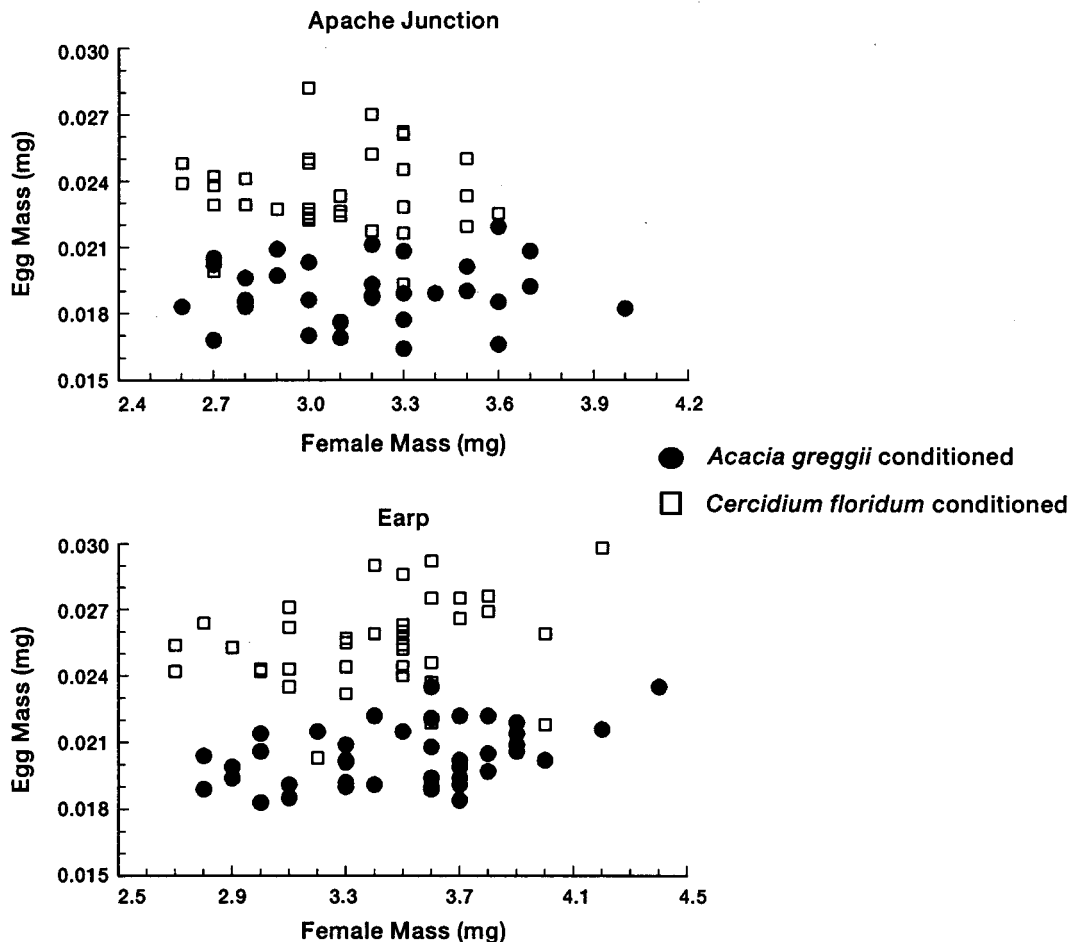
Although they emerged as adults sooner, progeny hatching from eggs laid by *C. floridum*-conditioned females emerged at approximately the same body size as progeny developing from eggs laid by *A. greggii*-conditioned females (Fig. 2, Table 1). In fact, although egg size differed more between treatments (within populations) than between the two *S. limbatus* populations examined, there was a larger average difference in body size between the two populations than between the two treatments within populations (Fig. 2).

There was no evidence that egg size affected the survivorship of larvae on *A. greggii*: eggs laid by *C. floridum*-conditioned females did not survive better than eggs laid by *A. greggii*-conditioned females (egg-to-adult survivorship was 0.92 ± 0.16 and 0.94 ± 0.11 for the Apache Junction population and 0.93 ± 0.11 and 0.96 ± 0.10 for the Earp population (mean \pm standard deviation), respectively; Wilcoxon signed-rank tests comparing family means, $P = 0.95$ for the Apache Junction population and $P = 0.08$ for the Earp population).

Regression analyses examining the relationship between egg size and progeny egg-to-adult development time within treatments showed some evidence that female progeny developing from large eggs developed faster than those developing from small eggs for the *A. greggii* conditioning treatment in both populations (Fig. 3, Table 2). However, among-family variation in egg size had no detectable effect on female development time in the *C. floridum* conditioning treatment for either population, or for male progeny in either treatment or population. With the exception of the *A. greggii* conditioning treatment in the Apache Junction population, egg size explained very little of the variation in progeny development time (for egg-size effects, $R^2 \leq 0.10$ for each sex, population, and treatment combination), as was observed in the egg-size manipulations described above.

Contrary to the results of the experimental manipulations, there was a tendency for female progeny developing from large eggs to emerge at a larger body size than those developing from small eggs (regression analyses, $P < 0.05$ for both treatments in the Earp population, not significant for either

Fig. 1. Effect of female oviposition experience on egg size of *Stator limbatus* from Apache Junction and Earp. Females that were first exposed to *Cercidium floridum* laid larger eggs than females first exposed to *Acacia greggii*. Analysis of covariance, with population and treatment treated as fixed effects and maternal body mass as a covariate (Type III sums of squares; SAS Institute Inc. 1985): population; $F_{[1,141]} = 15.3$, $P < 0.001$; treatment, $F_{[1,141]} = 317.5$, $P < 0.001$; maternal mass, $F_{[1,141]} = 10.0$, $P = 0.002$; $R^2 = 0.71$.



treatment in the Apache Junction population; Fig. 4, Table 2). However, egg size explained little of the variation in female body size (for egg-size effects, $R^2 < 0.15$ for each treatment and population), and there was no interpretable relationship between egg size and body size of male progeny in either treatment ($P > 0.25$ for each treatment and population).

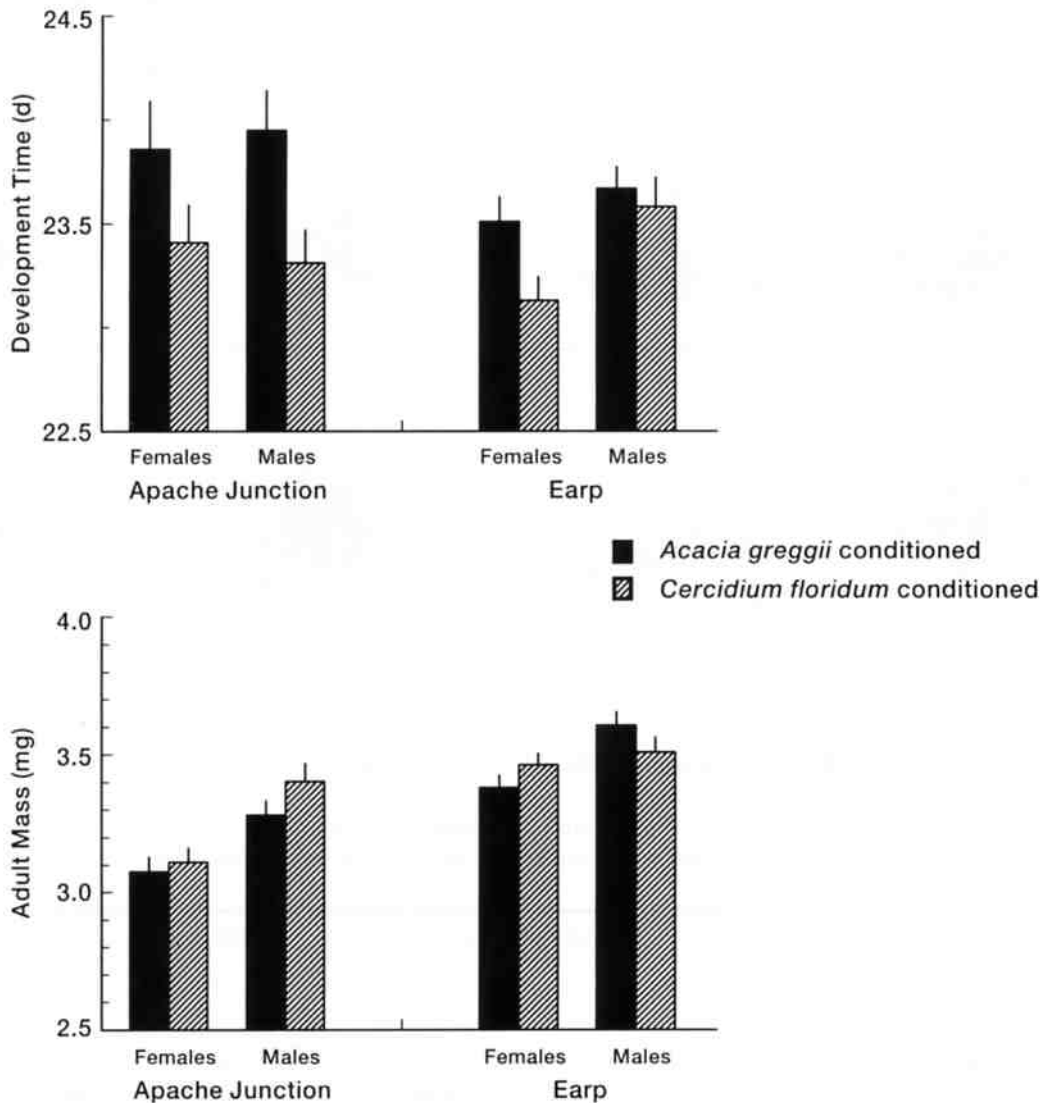
Discussion

The objective of this paper was to test the hypothesis that *S. limbatus* larvae developing from large eggs perform better (develop faster, attain a larger size, or survive better) than larvae developing from smaller eggs when reared on a high-quality host plant (*A. greggii*, on which larval survivorship is very high). Previous experiments with *S. limbatus* (Fox and Mousseau 1996) had demonstrated that larvae hatching from larger eggs have substantially higher egg-to-adult survivorship than larvae hatching from smaller eggs when reared on *C. floridum* (on which larval survivorship is very low). However, in the same experiments I was unable to demonstrate an advantage to larvae of hatching from a large egg when reared on *A. greggii*. The results of the experi-

ments described here suggest that egg size does in fact affect larval development time when larvae are reared on *A. greggii* (larvae hatching from large eggs emerge as adults sooner than larvae hatching from small eggs), but indicate that this egg-size effect is very small (e.g., explaining $< 7\%$ of the overall variance in development time). Also, there was little evidence that egg size affects the final adult size attained by progeny or the survivorship of progeny.

My results are consistent with previous results obtained with *S. limbatus* and many other insects, which have generally demonstrated that although egg size can have substantial effects on early progeny life histories (e.g., hatchling size/resources), progeny developing from small eggs compensate for reduced size/resources by developing longer to attain a genetically targeted body size. For example, in *Callosobruchus maculatus* (another seed beetle), older females lay smaller eggs (Fox 1993; Fox and Dingle 1994), and progeny hatching from these smaller eggs develop longer to emerge at the same body size as their siblings emerging from the larger eggs that were laid when their mother was younger. Similarly, female *S. limbatus* experiencing intense larval competition, and thus maturing smaller, lay smaller eggs than females reared at low densities, but progeny hatching

Fig. 2. Mean development times (egg to adult) and adult body mass of *S. limbatus* progeny developing from eggs laid by *C. floridum*- and *A. greggii*-conditioned females. See also the analyses of variance in Table 1.



from these smaller eggs develop longer to eventually attain the same adult body size as progeny hatching from larger eggs (Fox 1997). A further discussion of developmental plasticity and targeted body size is presented in Fox (1997).

Despite this trend for egg size to affect development time, but not final body size, in seed beetles and many other insects, numerous studies have detected a significant correlation between egg size and progeny body size across families (reviewed in Fox 1993; Fox and Mousseau 1996). However, such correlations are often confounded by genetic correlations among life-history characters and thus do not necessarily reflect cause and effect (Bernardo 1991; Fox 1994a). The results presented in this paper are consistent with this caution: although there was a positive correlation between egg size and progeny body size among families within treatments for one population (Fig. 4), there was no detectable effect of experimental treatment on progeny body size in either population, despite a highly significant effect of treatment on egg size. Thus, I suggest that for *S. limbatus*, the tendency for larger progeny to develop from larger eggs is a real (although

weak) relationship, but represents a combination of genetic and environmental correlations between a mother and her offspring because (i) body size and egg size of *S. limbatus* are both heritable (C.W. Fox, unpublished data) and (ii) the body size of the mother is positively correlated with the size of her eggs (Fox et al. 1995, 1997), such that (iii) the size of a mother's eggs is correlated with size of her offspring.

Although the results of this experiment suggest that egg size weakly affects larval development time, it is not possible to rule out effects of the experimental manipulations on factors other than egg size, such as egg composition. Unlike Sinervo and his colleagues (Sinervo 1990; Sinervo and Huey 1990), I did not physically manipulate yolk content, but tricked beetles into laying eggs of different sizes (as did Sinervo and Licht 1991a). Unfortunately, it is not known whether female *S. limbatus* modify only egg size, and not egg composition, in response to seed species (Fox et al. 1997). For some organisms (Bernardo 1996), including insects (Rossiter 1991), natural intraspecific variation in egg composition has been demonstrated to affect progeny growth

Fig. 3. Relationship between maternal egg size and mean progeny development time (including embryonic, larval, and pupal development) within each treatment and population. Each data point represents a single family (mean \pm SEM). The open circle labeled 28.5 (upper left panel) represents a family for which only one individual emerged and was considered an outlier and thus deleted from all statistical analyses.

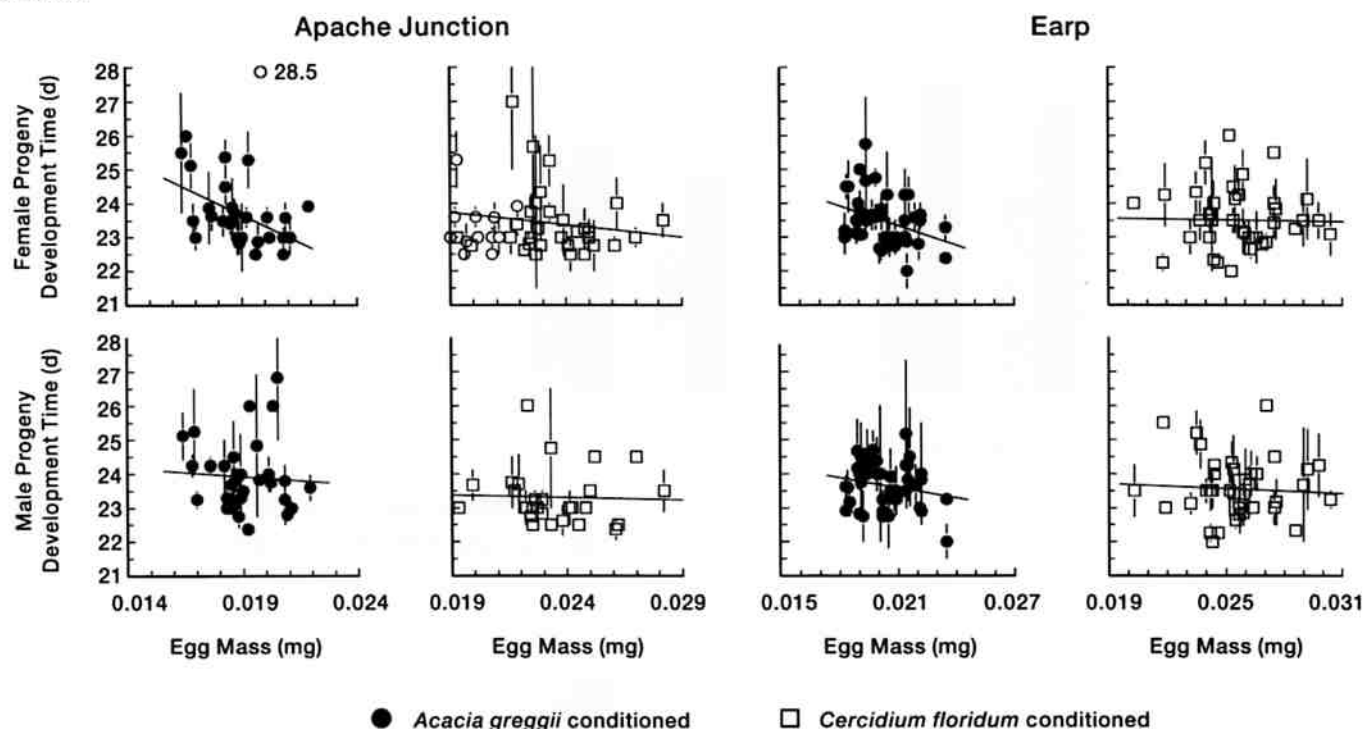


Table 1. Analyses of variance (Type III sums of squares; SAS Institute Inc. 1985) for the effect of female conditioning host on the egg-to-adult development time and adult body size of her progeny.

	Female progeny			Male progeny		
	df	F	P	df	F	P
Development time						
Population	1	3.9	0.05	1	0	0.978
Treatment	1	6.75	0.01	1	5.95	0.016
Population \times treatment	1	0.05	0.828	1	3.31	0.071
Error	136			133		
Adult mass						
Population	1	48.79	<0.001	1	15.09	<0.001
Treatment	1	1.56	0.213	1	0.05	0.819
Population \times treatment	1	0.26	0.609	1	3.97	0.048
Error	135			133		

Note: Each family mean was treated as a single data point for this analysis. Because of sexual dimorphism in development time and adult body size, separate analyses are presented for each sex. Population and treatment were each treated as a fixed effect. $R^2 = 0.07$ and 0.06 (female and male development time, respectively) and 0.27 and 0.13 (female and male adult mass, respectively). See also Fig. 2. Significant effects are in boldface type.

and development. Thus, differences in egg composition among treatments could potentially produce the treatment differences observed in this study. Nonetheless, in the absence of information on how maternal environment affects egg composition, and how egg composition affects larval development in *S. limbatus*, the results of this egg size manipulation experiment strongly suggest that egg size directly affects larval development time.

One important goal of this study was to determine why females do not lay even smaller eggs on *A. greggii* than they actually do. The size of eggs laid by females is generally argued to represent a balance between selection for large eggs, mediated through egg-size effects on progeny growth and development, and selection for small eggs due to a trade-off between egg size and egg number (Roff 1992; Stearns 1992). In previous studies, a large trade-off was demon-

Fig. 4. Relationship between maternal egg size and mean progeny body size (at adult emergence) within each treatment and population. Each data point represents a single family (mean ± SEM).

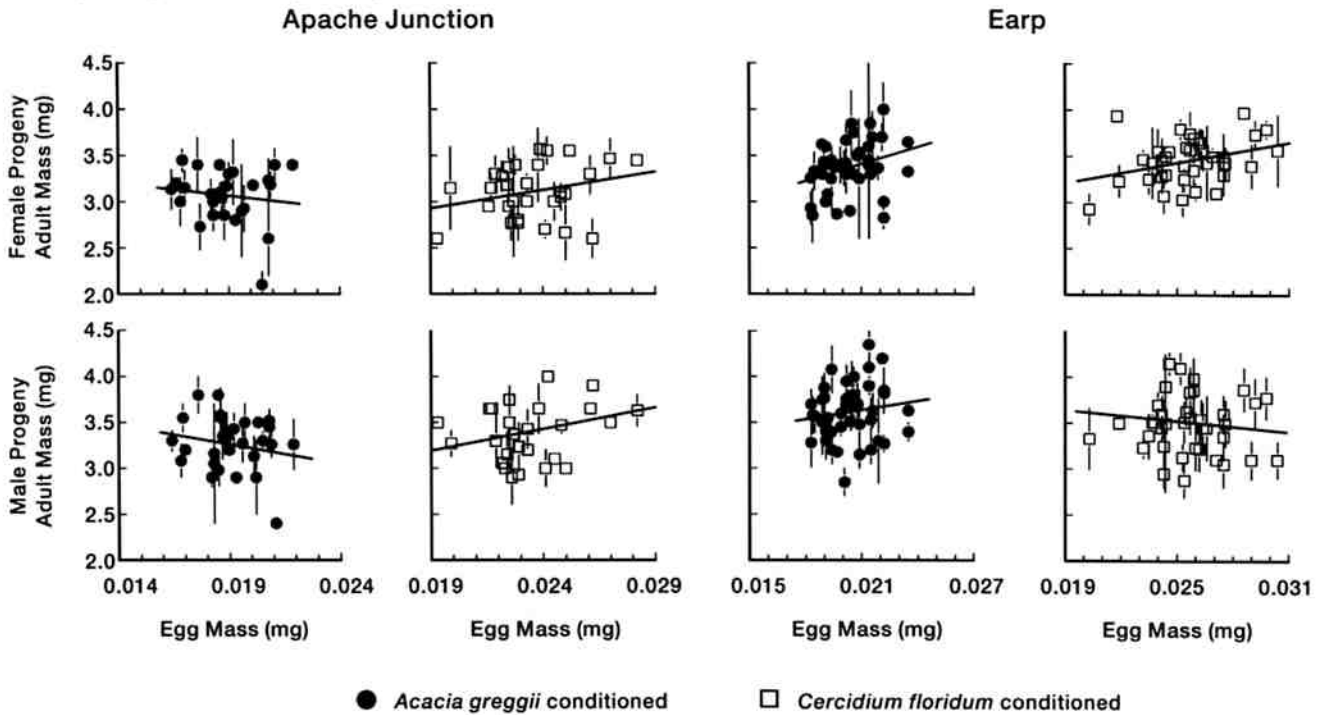


Table 2. Relationship between egg size (estimated egg mass) and egg-to-adult development time and adult body mass (see also Figs. 3 and 4).

	Apache Junction		Earp	
	<i>A. greggii</i> -conditioned	<i>C. floridum</i> -conditioned	<i>A. greggii</i> -conditioned	<i>C. floridum</i> -conditioned
	<i>R</i> ²	<i>R</i> ²	<i>R</i> ²	<i>R</i> ²
Egg-to-adult development time				
Female progeny	0.29**	0.01 ns	0.10*	0.01 ns
Male progeny	0.04 ns	0.00 ns	0.03 ns	0.01 ns
Body mass at adult emergence				
Female progeny	0.01 ns	0.08 ns	0.11*	0.15*
Male progeny	0.00 ns	0.06 ns	0.01 ns	0.01 ns

Note: For the analyses, each family mean was treated as a single data point. *, *P* < 0.05; **, *P* < 0.01. *P* values have not been corrected for multiple comparisons.

strated between egg size and egg number in *S. limbatus* (Fox et al. 1997), but I was unable to demonstrate an advantage to developing from a larger egg when larvae are reared on *A. greggii* (Fox and Mousseau 1996), suggesting that selection should favor females that lay even smaller eggs, and thus more eggs, than the population mean. In this study, I found at most a small advantage to larvae of developing from a larger egg: they reach their targeted emergence body size slightly sooner. However, my results also suggest another cost to laying large eggs: they take longer to hatch than small eggs (see also Steele 1977; Guisande and Gliwicz 1992; Bernardo 1996). The large eggs laid by *C. floridum*-conditioned females took ≈ 8 h longer to hatch than the small eggs laid by *A. greggii*-conditioned females, which reflects a ≈ 10% increase in embryonic development time. This 8 h may represent a cost to *S. limbatus* in terms of larval mortal-

ity in nature. Throughout most of their larval development period, *S. limbatus* larvae are well protected from predators and parasites because they develop encased inside a protective seed. Aside from mortality due to rodent predation on seeds, the beetles are susceptible to natural enemies primarily during the egg stage, when they are attacked by parasitoid wasps (Hetz and Johnson 1988; Siemens and Johnson 1992). Thus, an increase in embryonic development time may translate into increased susceptibility to egg parasitoids. Similarly, an increase in embryonic development time may increase mortality due to egg trampling by ovipositing females. Research on another seed beetle, *Callosobruchus maculatus* (Utida 1941; Smith and Lessells 1985), suggests that eggs exposed longer to trampling may suffer higher mortality than eggs that hatch quickly. These hypotheses, however, are as yet untested.

Thus, the puzzle of why *S. limbatus* populations do not lay even smaller eggs on *A. greggii* remains. I suspect that three factors may contribute to the solution. First, constraints on egg-size evolution may be imposed by positive genetic correlations between egg sizes across hosts, so that selection for large eggs on *C. floridum* results in a correlated increase in the size of eggs laid on *A. greggii*. This would especially constrain the evolution of egg size on *A. greggii* for populations using both *C. floridum* and *A. greggii* simultaneously (such as the two populations studied here), since selection for large eggs on *C. floridum* is intense (Fox and Mousseau 1996), but may also constrain the evolution of egg size in populations restricted to *A. greggii* if gene flow between host-associated populations is relatively high. Host plants for *S. limbatus* are present throughout much of the southwestern United States, suggesting the potential for high gene flow between geographic areas.

High larval density may also select for larger eggs on *A. greggii*. Most of my laboratory experiments on *S. limbatus* (including those described here) have been conducted under controlled laboratory conditions, with beetles reared at low density (generally one beetle per seed; Fox and Mousseau 1996; Fox et al. 1997). However, in nature larvae frequently develop at densities greater than one individual per seed (Mitchell 1977; Siemens and Johnson 1992), which results in intense competition among larvae (Fox et al. 1996; Fox 1997); larvae reared at high density emerge sooner and smaller than those reared at low density. Possibly, larvae developing from large eggs have an advantage over those developing from small eggs at high larval density.

A third reason why female *S. limbatus* do not lay smaller eggs on *A. greggii* may be that while the consequences of egg size for progeny growth are very small within the size range of eggs naturally laid on *A. greggii*, below a threshold size larval performance may decrease rapidly with decreasing egg size. This is observed on *C. floridum*: there appear to be two thresholds in egg size, one below which larval mortality is nearly 100% and another above which larval survivorship is nearly 100% (Fox and Mousseau 1996; Fox et al. 1997). Possibly, egg size of *A. greggii* is maintained above a similar lower threshold, giving the impression that egg size has only a modest effect on progeny. Unfortunately, because *S. limbatus* eggs have not yet been successfully reduced in size experimentally (puncturing eggs with a needle kills them), this hypothesis is not yet testable. Hormonal manipulations similar to those applied by Sinervo and Licht (1991a) may provide a mechanism for testing this hypothesis in the future.

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