EGG SIZE PLASTICITY IN A SEED BEETLE: AN ADAPTIVE MATERNAL EFFECT

CHARLES W. FOX,* MONICA S. THAKAR, AND TIMOTHY A. MOUSSEAU

Department of Biological Sciences, University of South Carolina, Columbia, South Carolina 29208

Abstract.—In the seed beetle, Stator limbatus, the fitness consequences of egg size vary substantially among host plants. There is intense selection for laying large eggs when larvae will develop on seeds of Cercidium floridum (caused by high mortality penetrating the seed coat) but selection for laying small eggs when larvae will develop on seeds of Acacia greggii (caused by very low mortality penetrating the seed coat and an egg size/egg number trade-off). We test the hypothesis that host-associated variation in egg size within populations of S. limbatus represents an adaptive maternal effect in which females adjust egg size in response to host species. In laboratory experiments, S. limbatus females laid significantly larger and fewer eggs on C. floridum than on A. greggii. When switched between hosts, females readjusted egg size, producing progressively larger eggs on C. floridum and smaller eggs on A. greggii. When conditioned to lay either small eggs (on A. greggii) or large eggs (on C. floridum), and then forced to lay on C. floridum, females conditioned on C. floridum laid eggs that had substantially higher survivorship than eggs laid by females conditioned on A. greggii. These experiments demonstrate that egg size is an adaptively plastic character in S. limbatus.

Phenotypic variation in natural populations is influenced by both genetic and environmental variation among individuals. One important source of environmental variation is the maternal effect: nongenetic influences of maternal phenotype or environment on offspring phenotypes (Mousseau and Dingle 1991a, 1991b; Riska 1991). Maternal effects can be adaptive for organisms in heterogeneous environments (Saunders 1982; Danks 1987; Roach and Wulff 1987; Lacey 1991; Mousseau and Dingle 1991a, 1991b; Reznick 1991; Sinervo 1991; Fox et al. 1995b). For example, some maternal effects have likely evolved as mechanisms for "transgenerational phenotypic plasticity" (Mousseau and Dingle 1991b), whereby a mother that experiences a predictive environmental cue (e.g., high or low host density, short or long photoperiod) can program a developmental switch in her offspring appropriate for the environmental conditions predicted by the cue. However, despite their potential ecological and evolutionary importance, adaptive maternal effects have received less attention than other types of adaptations to heterogeneous environments.

In this context, egg size is a particularly important life-history trait because it

* To whom correspondence should be addressed. Present address: The Louis Calder Center of Fordham University, 53 Whippoorwill Road, Box K, Armonk, New York 10504; E-mail: Fox@-murray.fordham.edu.

is simultaneously a maternal and offspring character (Sinervo 1991); eggs are produced by mothers but also determine initial offspring resources/size. Growth and survival are profoundly influenced by the amount and quality of resources allocated to offspring by mothers (Roach and Wulff 1987; Platenkamp and Shaw 1993). In animals, progeny developing from large eggs generally grow faster, attain larger size, and have higher survivorship than progeny developing from small eggs (reviews in Fleming and Gross 1990; Kaplan 1991; Reznick 1991; Fox 1994a, 1994b). However, mothers laying large eggs must lay fewer eggs because of the trade-off between size and number of progeny (Smith and Fretwell 1974; Fleming and Gross 1990; Berrigan 1991), which results in an egg size that is a balance between selection for large eggs and selection for many eggs.

In natural populations, the consequences of egg size variation depend on environmental conditions, with fitness differences between large and small eggs generally greatest in adverse environments (Janzen 1977; Braby 1994; Fox and Mousseau 1996). Thus, selection favors eggs of different sizes in different environments, which results in substantial geographical variation in egg size in many organisms (Fleming and Gross 1990; Rowe 1994). For example, egg size varies with latitude (Rounsefell 1957; Harvey 1983; Fleming and Gross 1990; Miller et al. 1991; Garcia-Barros 1992, 1994; Beacham and Murray 1993; Rijnsdorp and Vingerhoed 1994), altitude (Baur 1990), season (Bagenal 1971; Rijnsdorp and Vingerhoed 1994), and temperature (Devauchelle et al. 1987), and this geographical variation is often genetic (e.g., Mashiko 1992). In temporally and spatially heterogeneous environments, selection variably favors large eggs and small eggs, depending on the time and location of oviposition. Alternatively, selection may favor egg size plasticity (Kawecki 1995; but see McGinley et al. 1987), whereby a mother that experiences a predictive environmental cue can variably allocate resources to her offspring appropriate for the conditions predicted by the cue (Mousseau and Dingle 1991a).

In the seed beetle, *Stator limbatus* (Coleoptera: Bruchidae), the fitness consequences of egg size vary substantially among host plants. On *Cercidium floridum* larval survivorship is very poor (generally <40%–50%; Siemens and Johnson 1990; Fox et al. 1994, 1995a), and larvae from large eggs survive substantially better than larvae from small eggs (linear regression, effect of egg size on egg-to-adult survivorship, $r^2 = 0.67$–0.70) (Fox and Mousseau 1996), selecting for large eggs. On *Acacia greggii,* however, larval survivorship is very high (95%–99%) (Fox et al. 1994, 1995b), and there is no effect of egg size on survivorship because almost all larvae survive to adult ($r^2 = 0.00$) (Fox and Mousseau 1996). Thus, although there is intense selection for laying large eggs when larvae will develop on *C. floridum* (because small eggs almost all die), there is selection for laying small eggs when larvae will develop on *A. greggii* (because small eggs survive as well as large eggs on *A. greggii,* but females laying small eggs can lay more eggs because of an egg size/egg number trade-off; see data presented later).

Population comparisons support these predictions about differing selection on *C. floridum* and *A. greggii;* populations collected from *C. floridum* lay fewer and larger eggs than populations collected from *A. greggii* (Fox et al. 1995a; Fox and Mousseau 1996), as expected if selection favored laying larger eggs on *C. flor-*

idum than on *A. greggii*. It is also interesting that eggs laid on *C. floridum* in nature are larger than eggs laid on *A. greggii* even when host plants are sympatric (i.e., within beetle populations) (C. W. Fox, unpublished data). This latter observation is consistent with the hypothesis that *S. limbatus* populations are genetically substructured, consisting of genetically differentiated host-associated subpopulations (Siemens and Johnson 1990). Alternatively, within-population variation in egg size may be environmentally determined, with females responding to host species by laying larger eggs on *C. floridum* and smaller eggs on *A. greggii*. Because female *S. limbatus* delay oviposition for at least 24 h after emergence, during which time they finish maturing eggs (C. W. Fox, unpublished data), they are often in contact with their oviposition substrate (host plant) during egg maturation, which provides the opportunity for facultative responses to host species. Because selection favors large eggs on *C. floridum* and small eggs on *A. greggii,* selection will favor females that adjust egg size, laying large eggs on *C. floridum* and small eggs on *A. greggii.*

Here, we demonstrate that host-associated variation in egg size *within* populations of *S. limbatus* represents an adaptive maternal effect in which females adjust egg size in response to host species by laying larger eggs on *C. floridum* than on *A. greggii*. We then demonstrate that this plasticity of egg size is adaptive by examining survivorship of both "*Acacia*-size" and "*Cercidium*-size" eggs on *C. floridum* to determine whether adjustment of egg size affects survivorship or development of larvae on this host.

MATERIAL AND METHODS

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 geographical range, *S. limbatus* has been reared from seeds of more than 50 plant species in at least nine genera. In the United States, and particularly in Arizona, *S. limbatus* 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. For hosts that are indehiscent, such as *C. floridum,* beetles attack seeds almost entirely through emergence holes of other bruchids, such as *Mimosestes* species (Coleoptera: Bruchidae), 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, unpublished data).

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 their mother has chosen for them. In the lab, mating and egg laying begin approximately 24–48 h postemergence. Beetles require only a single seed to complete development and reproduce. Thus, neither food nor water supplementation is necessary for the following lab experiments.

Further details on the ecology of these beetles and their host plants can be found elsewhere (Siemens and Johnson 1990; Siemens et al. 1991, 1992; Fox et al. 1994, 1995b).

Study Populations

Beetles for these experiments were collected from two localities in central Arizona. On October 16, 1994, beetles were collected from *C. floridum* along Scottsdale Highway, 1.7 mi north of Bell Road (behind the Scottsdale Well), in Scottsdale, Arizona. On October 17, 1994, beetles were collected from *C. floridum* and *C. microphyllum* from numerous locations in Apache Junction, Arizona. These two populations are <50 km apart, with *C. floridum* distributed throughout the intervening region. Thus, although these populations differ in the host plants available to them (the Scottsdale population is restricted largely to *C. floridum*, with some access to *C. microphyllum*, whereas the Apache Junction population has access to *C. floridum*, *C. microphyllum*, and *A. greggii*), there is likely high gene flow between populations. Beetles and seed stock were both collected by picking mature seed pods from more than 25 *C. floridum* (Scottsdale) and more than 25 *C. floridum* and *C. microphyllum* plants (Apache Junction). Mature pods were transferred to the lab, and seeds containing beetles were separated from uninfested seeds. Seeds containing entrance or emergence holes of other bruchids (such as *Mimosestes* spp.) were discarded. We estimate that both laboratory populations were initiated with more than 300 field-collected individuals.

Egg Size Plasticity

For comparative purposes, this experiment was performed on both the Scottsdale and Apache Junction populations of *S. limbatus*. Both populations were maintained on *A. greggii* for three generations before this experiment, at 29°–30°C, 15L:9D.

To test the hypothesis that *S. limbatus* egg size is a phenotypically plastic response to host species, virgin males and females were collected from isolated seeds of *A. greggii* 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 30-mm petri dish containing 12 *A. greggii* seeds (both populations), 12 *C. floridum* seeds (both populations), or both six *A. greggii* and six *C. floridum* seeds (Scottsdale population only). Dishes were checked for eggs every 12 h until the female died. Females oviposit directly onto seeds, so seeds containing eggs were removed and replaced with clean seeds of the same species. Egg size was recorded for all eggs laid within the first 12 h after egg laying was initiated (egg length and width). Both egg length and egg width are positively correlated with egg weight (egg length, $R^2 = 0.88$; egg width, $R^2 = 0.61$) (Fox and Mousseau 1996). Because eggs are glued to seeds and removing them from the seeds is very time-consuming and often destructive, weighing eggs is not practical.

To confirm that observed differences in egg size among hosts were not due to differences in the length of egg maturation resulting from avoidance of oviposition on either host, we examined the effect of seed species on egg size following a short period of host deprivation. Virgin males and females were collected from isolated seeds of *A. greggii* 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 30-mm petri dish without any seeds. After 48 h of host deprivation, beetles were provided with either 12 *A. greggii* seeds or 12 *C. floridum* seeds. All females laid eggs within 12 h of seed addition, regardless of host. This experiment was performed on the Scottsdale population only, after three generations of laboratory rearing.

The Phenology of Egg Size Plasticity

This experiment was designed to provide insights into the physiological mechanism underlying plasticity in egg size and the time course of acclimation to a newly encountered host. It was performed using Scottsdale beetles after four generations of laboratory rearing on *A. greggii* at 29°–30°C, 15L:9D.

As done previously, virgin males and females were collected from isolated seeds of *A. greggii* 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 30-mm petri dish containing either eight *A. greggii* seeds or eight *C. floridum* seeds. Dishes were checked for eggs every 12 h until the female laid at least one egg. Treatment females were then switched to a new seed species, from *A. greggii* to *C. floridum* or from *C. floridum* to *A. greggii*. As a control, approximately half of the females were left on their original host. Again, dishes were checked for eggs every 12 h until the females died. Seeds bearing eggs were removed and replaced with clean seeds of the same species. Egg size was recorded for three eggs (haphazardly selected from the dish) in each 12-h interval.

The Adaptive Significance of Egg Size Plasticity

This experiment was performed using Scottsdale beetles after five generations of laboratory rearing on *A. greggii*.

To test the hypothesis that adjusting egg size is adaptive, females were conditioned to lay either large or small eggs, and then forced to lay on *C. floridum*. To manipulate egg size, we took advantage of the result from the prior experiment that the egg size response to a new host takes approximately 36 h. Virgin males and females were collected from isolated seeds of *A. greggii* 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 30-mm petri dish containing either eight *A. greggii* seeds or eight *C. floridum* seeds. Dishes were checked for eggs every 12 h until the female laid at least one egg. Females were then switched to 15 *C. floridum* seeds and allowed to lay eggs for 24 h. All progeny were reared to adult at densities of one beetle per seed (excess eggs were scraped from the seed), 29°–30°C, 15L:9D. The size of eggs on *C. floridum* was recorded for each female.

RESULTS

In both populations, female *Stator limbatus* confined on *Cercidium floridum* laid significantly larger eggs than females confined on *Acacia greggii* (fig. 1; tables 1, 2). Females also laid substantially fewer eggs on *C. floridum* (fig. 2; table 1), as expected if a trade-off between egg size and egg number exists. A trade-off between egg size and egg number is also evident from the negative correlation between egg size and egg number, after controlling for body size, within each treatment (table 3).

Because eggs are glued to seeds and difficult to keep intact when removing from the seed, we have measured egg dimensions (length and width) rather than estimated volume. Thus, one possible explanation for the observed host effects on egg size is that females lay differently shaped eggs on each host. However, three lines of evidence indicate that this is not the case. First, females that laid larger eggs (measured as length and width) also laid fewer eggs (table 3). Second, when females were presented with both *C. floridum* and *A. greggii* simultaneously, there was no difference in the length or width of eggs laid on the two seeds (table 2; Wilcoxon signed-rank test, $P > .05$, $N = 25$). Finally, when females were denied access to host seeds for 48 h (longer than required to mature eggs), such that egg maturation occurred without any interaction with their future oviposition host, the effects of oviposition host on egg length and width disappeared (table 2; ANCOVAs, treatment effect not significant for either length or width; $P > .05$ for each; $N = 30$ on each host). Also note that, following host deprivation, the eggs laid by females on both *C. floridum* and *A. greggii* were significantly smaller than eggs laid on *C. floridum* by nondeprived females (Mann-Whitney U-test, $P < .05$) but not significantly different from the size of eggs laid on *A. greggii* by nondeprived females ($P > .05$).

In the host switch experiment, as in the earlier experiment, females confined on *A. greggii* until their first egg laid substantially smaller eggs than females first confined on *C. floridum* (fig. 3A, 0 h bar). When switched to a new host (from *A. greggii* to *C. floridum* or from *C. floridum* to *A. greggii*), the females had an egg size that stayed relatively constant for the next 24–36 h. However, females then began to readjust egg size, producing progressively larger eggs on *C. floridum* and smaller eggs on *A. greggii* (repeated-measures ANOVA, significant treatment-by-day interaction, $P < .001$). By 48 h after the shift to their new host, the treatment difference in egg size had disappeared, and by 60 h after the switch to a new host, females were again laying larger eggs on *C. floridum* than on *A. greggii* (fig. 3A). In contrast, egg size of females that were not switched to a new host actually continued to diverge (although only slightly) throughout their lifetime (fig. 3B; repeated-measures ANOVA, significant treatment-by-day interaction, $P < .05$).

Females conditioned to lay eggs on *A. greggii*, and then forced to lay on *C. floridum*, laid substantially smaller eggs on *C. floridum* than females conditioned to lay on *C. floridum* (egg length, 5.49 ± 0.03 vs. 5.98 ± 0.02 mm/10; egg width, 4.03 ± 0.02 vs. 4.42 ± 0.02 mm/10). Eggs from these *A. greggii* conditioned females subsequently had very low egg-to-adult survivorship on *C. floridum* (0.3%
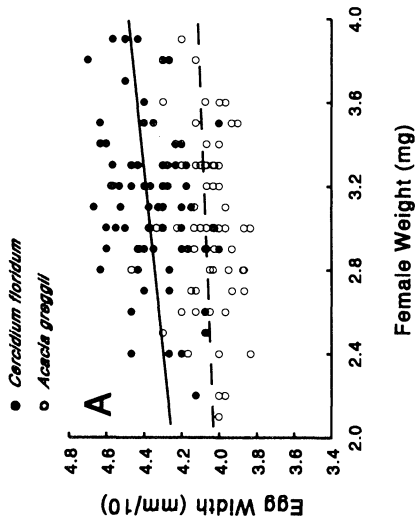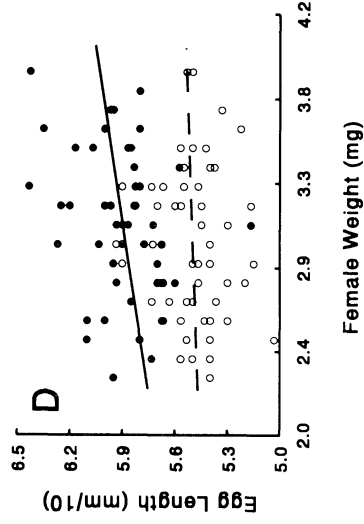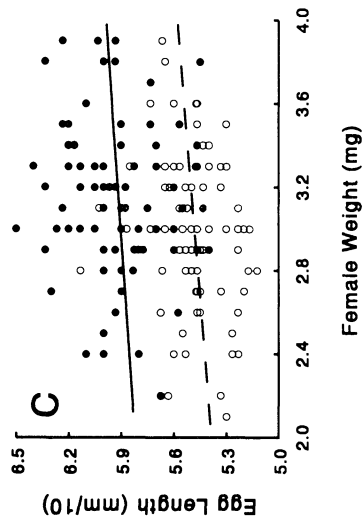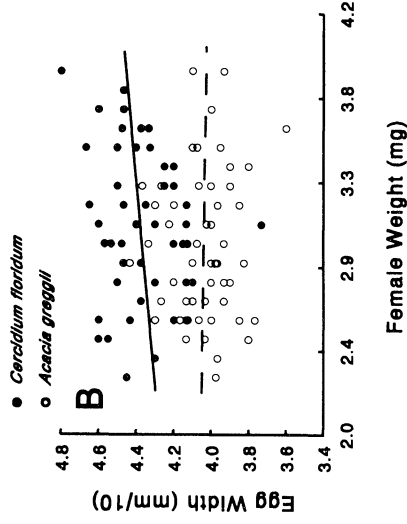
FIG. 1.—Size of eggs laid by females presented with either *Acacia greggii* or *Cercidium floridum* seeds. Females lay much larger eggs on *C. floridum*. Table 1 presents ANCOVAs. *A*, Scottsdale population, egg width; *B*, Apache Junction population, egg width; *C*, Scottsdale population, egg length; and *D*, Apache Junction population, egg length. Sample sizes: Scottsdale population, *N* = 77; Apache Junction population, *N* = 56.

TABLE 1

ANCOVAs Examining the Effects of Seed Species on Egg Size and Lifetime Fecundity

POPULATION	EGG LENGTH			EGG WIDTH			LIFETIME FECUNDITY		
	df	F	P	df	F	P	df	F	P
Scottsdale:									
Host species	1	129.2	***	1	143.4	***	1	80.4	***
Female size	1	3.3	NS	1	6.1	*	1	20.3	***
Male size	1	.0	NS	1	.0	NS	1	18.7	***
		$R^2 = .51$			$R^2 = .47$			$R^2 = .53$	
Apache Junction:									
Host species	1	89.3	***	1	82.2	***	1	81.2	***
Female size	1	3.1	NS	1	.5	NS	1	25.0	***
Male size	1	.1	NS	1	.3	NS	1	22.4	***
		$R^2 = .49$			$R^2 = .52$			$R^2 = .43$	

NOTE.—Analyses using SAS PROC GLM, Type III sums of squares (SAS 1985). Host species is treated as a fixed effect and female size and male size as covariates. Male size is included in the model because of male effects on female fecundity and egg size detected elsewhere (Fox et al. 1995b). See also figures 1 and 2. NS, not significant.
* $P < .05$.
*** $P < .001$.

TABLE 2

The Size of Eggs ± SEM (N = number of females) Laid by Female Stator Limbatus

	Acacia greggii (AG)	Cercidium floridum (CF)	AG vs. CF
Presented either A. greggii or C. floridum within 12 h of adult emergence:			
Scottsdale population:			
Egg length	5.49 ± .02 (77)	5.92 ± .03 (75)	***
Egg width	4.07 ± .01 (77)	4.38 ± .02 (75)	***
Apache Junction population:			
Egg length	5.50 ± .02 (56)	5.90 ± .03 (48)	***
Egg width	4.04 ± .02 (56)	4.38 ± .03 (48)	***
Both A. greggii and C. floridum presented simultaneously:			
Egg length	5.75 ± .05 (25)	5.79 ± .05 (25)	NS
Egg width	4.36 ± .04 (25)	4.40 ± .04 (25)	NS
Presented either A. greggii or C. floridum following 48 h of host deprivation:			
Egg length	5.61 ± .04 (30)	5.57 ± .03 (30)	NS
Egg width	4.11 ± .03 (30)	4.10 ± .02 (30)	NS

NOTE.—Length and width of eggs ± SEM (N). For the first and last treatments here (either AG or CE presented within 12 h of adult emergence and following 48 h of host deprivation, respectively), host effects were examined by ANCOVA with female body weight as the covariate. For the second treatment (both AG and CF presented simultaneously), comparisons between hosts are by Wilcoxon signed-rank tests; $P > .05$ for each. NS, not significant.
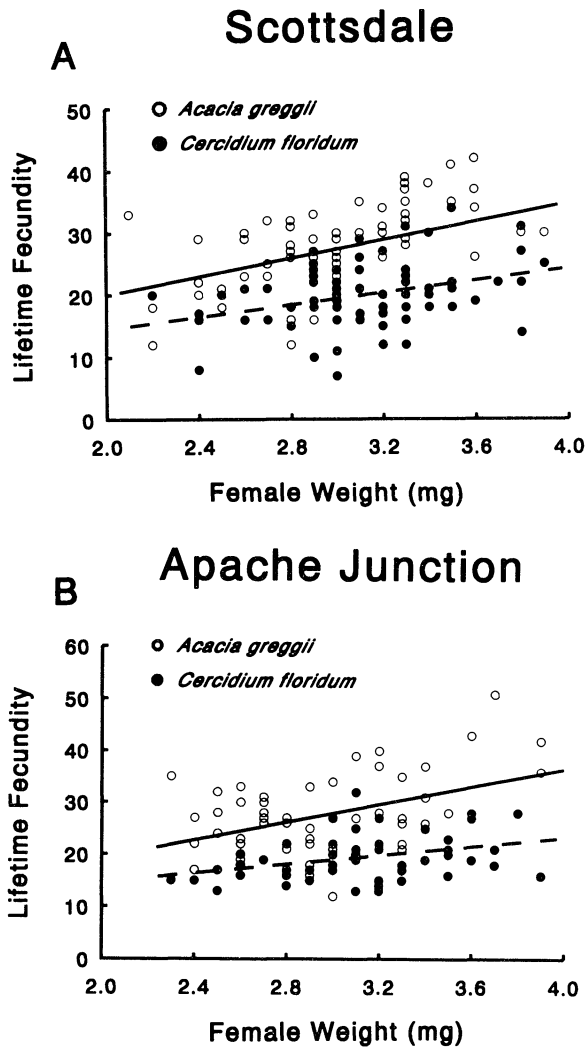*** $P < .001$.

FIG. 2.—Lifetime fecundity of females presented with either *Acacia greggii* or *Cercidium floridum*. The treatment that lays the largest eggs (*C. floridum*) also lays the fewest eggs. Table 1 presents ANCOVAs. *A*, Scottsdale population; *B*, Apache Junction population. Sample sizes are the same as those cited in figure 1.

± 0.2%, $N = 86$ families, 1,035 eggs; average survivorship is the mean survivorship across families rather than the number of emergers/number of eggs), while eggs laid by females that were conditioned on *C. floridum* had substantially higher egg-to-adult survivorship on this host (23.7% ± 2.1%; Mann-Whitney *U*-test, $P <$ .0001, $N = 90$ families, 754 eggs). Also, egg-to-adult survivorship was positively correlated with both egg length and width within the *C. floridum*–conditioned treatment (length, $R^2 = 0.14$; width, $R^2 = 0.14$; $P < .01$ for each). This latter analysis was not possible for the *Acacia*-conditioned treatment because there

TABLE 3

REGRESSION ANALYSIS DEMONSTRATING A TRADE-OFF BETWEEN EGG SIZE AND EGG NUMBER
IN TWO POPULATIONS OF *STATOR LIMBATUS*

Population/Host	Egg Number = Female Weight + Male Weight + Egg Length (Partial R^2)	Egg Number = Female Weight + Male Weight + Egg Width (Partial R^2)
Scottsdale on *Acacia greggii:*		
Female weight	.16***	.13**
Male weight	.19***	.15***
Egg size	−.16***	−.07*
Scottsdale on *Cercidium floridum:*		
Female weight	.29***	.27***
Male weight	.18***	.18***
Egg size	−.43***	−.28***
Apache Junction on *A. greggii:*		
Female weight	.39***	.32***
Male weight	.21***	.22***
Egg size	−.28***	−.17**
Apache Junction on *C. floridum:*		
Female weight	.22**	.19***
Male weight	.29***	.32***
Egg size	−.22**	−.22**

NOTE.—Regression analyses were done using SAS PROC REG, Type II sums of squares (SAS 1985). The sign on the partial R^2 reflects the sign on the coefficient (and thus the direction of the relationship).
* $P < .05$.
** $P < .01$.
*** $P < .001$.

were only four survivors (from three families); survivorship of 83 families was zero.

DISCUSSION

Egg size variation among females has long been known to be influenced by both genetic and environmental effects (review in Fox 1994b), whereas variation *within* females is commonly attributed to variation in nutrient status or age, each of which prevent a female from laying her optimal egg size (reviews in Fox 1993; Fox and Dingle 1994). The experiments presented here demonstrate that within and among female variation in egg size partly represents an adaptive response to a changing optimal egg size; female *Stator limbatus* variably allocate resources to offspring in a manner likely to increase individual fitness by laying large eggs on *Cercidium floridum* (on which large eggs have higher larval survivorship than small eggs) and laying small eggs on *Acacia greggii* (on which egg size does not affect offspring survivorship). This plastic egg size is adaptive in *S. limbatus*. Females conditioned to lay large eggs produce eggs that have substantially higher fitness on *C. floridum* than females conditioned to lay small eggs, whereas females laying small eggs on *A. greggii* lay substantially more eggs than females laying large eggs, because of an egg size/egg number trade-off that is independent of maternal body size.

Phenotypically plastic egg size in *S. limbatus* is not the result of female reluctance to lay eggs on *C. floridum*. Because larval survivorship is very low on *C. floridum*, we might expect females to evolve avoidance of *C. floridum* in prefer-
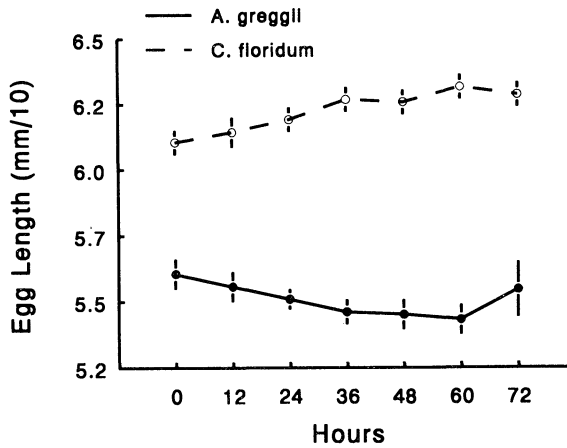
A
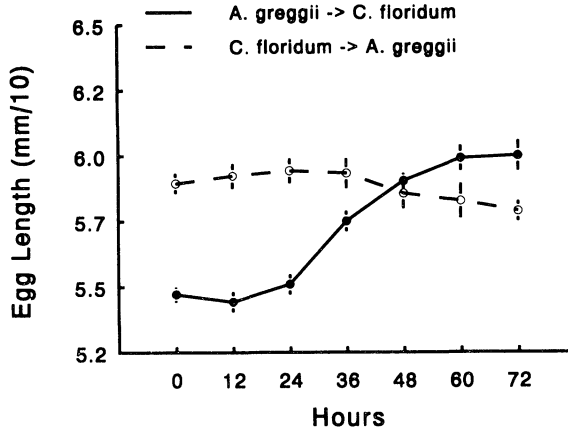
B

Fig. 3.—The effect of switching seed species on egg size (Scottsdale population). *A,* Females confined on either *Cercidium floridum* or *Acacia greggii* until they laid their first egg, and then switched to the other host; *B,* females confined on a single host until death. In each experiment, Hour = 0 is the time period during which females laid their first egg.

ence of *A. greggii*. Such reluctance to oviposit on *C. floridum* would result in prolonged egg retention when encountering *C. floridum* and thus possibly increased resources allocated to eggs. However, despite the high mortality of eggs laid on *C. floridum,* paired preference tests indicate that females either prefer to oviposit on *C. floridum* (when compared with *A. greggii*) or show no preference for either host (Fox et al. 1994), which indicates that female *S. limbatus* are not reluctant to lay on *C. floridum*. Also, when deprived of hosts and thus allowed additional time for egg maturation, initial eggs are small (i.e., not significantly

different from egg sizes on *A. greggii* but significantly smaller than eggs laid on *C. floridum* by non-host-deprived females; table 2).

Our demonstration that egg size is phenotypically plastic is consistent with predictions of theoretical models demonstrating that larger offspring should be produced when conditions for juvenile growth and survivorship are poor (Sibly and Calow 1983; Parker and Begon 1986). Because environmental conditions for progeny development generally vary spatially and temporally within populations, adaptive plasticity is expected to evolve for egg size. However, adaptive plasticity in progeny size has been demonstrated for only a few animals. For example, some cladocerans respond to reduced food availability by producing larger offspring (Smith 1963; Perrin 1989; Guisande and Gliwicz 1992). Also, *Callosobruchus maculatus* (another seed beetle) responds to population density by laying larger eggs at higher density (although the observed effect was very small, 1%–4%; Kawecki 1995). To our knowledge, egg size adjustment in *S. limbatus* is the first demonstration of an adaptive response to variation in host-plant species through adjusting progeny size and the first demonstration of egg size plasticity in response to resource quality that is not mediated by female nutritional status.

The physiological mechanism for egg size adjustment in *S. limbatus* is not known. Observations on *Drosophila* suggest that increases in egg size with decreasing temperature are due in part to a longer retention of eggs during oogenesis (Avelar 1993). Prolonging retention of eggs during oogenesis is not likely responsible for the increase in egg size observed in *S. limbatus* because, when females were forced to delay oviposition because of host deprivation, they produced small eggs (not different in size from eggs normally laid on *A. greggii* but significantly smaller than eggs laid on *C. floridum*) regardless of rearing host.

Although female *S. limbatus* respond to early adult experience by adjusting egg size, females can readjust egg size following encounters with a new host species. However, this readjustment was not immediate upon encounter with the new host; females required interaction with their oviposition substrate for at least 24–36 h before readjusting egg size. This is approximately the time required for a female to mature an egg (C. W. Fox, unpublished data), which suggests that egg size is fixed early in egg maturation. Also, the readjustment of egg size was asymmetrical; switching from *A. greggii* to *C. floridum* resulted in substantial increases in egg size, while switching from *C. floridum* to *A. greggii* resulted in only a modest decrease in egg size. Possibly, this asymmetry is a result of anatomical or physiological constraints, although the potential form of these constraints is unknown. Alternatively, there may be little selection on decreasing egg size following a host shift. At the population level, female *S. limbatus* encounter both *C. floridum* and *A. greggii,* and a female likely cannot predict which host she will lay on until encountering the host (resulting in selection for plasticity). However, at the individual level, we suspect that encounters with multiple host plants (host switching) by a single female are uncommon in nature because of the abundance of fruits produced by each individual host plant (i.e., patchy distribution of seeds). Thus, readjusting egg size may generally be unnecessary in nature, such that the asymmetry in egg size readjustment may be at most under very weak selection and thus represent an artifact of the physiological/morphological mechanism by which females respond to hosts.

The adjustment of egg size in response to host species raises concerns about the use of some single-host (no-choice) designs (Singer 1986) for the estimation of oviposition preference of herbivorous insects. For example, average oviposition preference of seed beetle populations is often estimated by confining females on a single host for a fixed unit of time or until death (multiple females on each host), with preference defined as the mean number of eggs laid on each host (Wasserman 1986). However, if females respond to host species by adjusting egg size, egg number and the resulting estimate of preference may be unrepresentative of behavioral variation. Also, among-population variation in oviposition preference may reflect variation in the ability to adjust egg size rather than behavioral variation. Future studies of oviposition preference, particularly those using these seed beetles, should compare egg size between treatments to control for biases introduced by egg size plasticity.

We speculate that the ability of *S. limbatus* mothers to ameliorate variation in early larval survival via egg size plasticity in response to a heterogeneous environment may account, at least in part, for this species' generalist life history. Most herbivorous insects are relatively specialized, feeding on few of the plant taxa available to them (Fox and Morrow 1981). This is particularly obvious among seed beetles (Bruchidae) in which most species feed on one or a few species, generally in a single genus (e.g., Johnson and Kingsolver 1976; Johnson et al. 1989). *Stator limbatus* is unusual among seed beetles in that it is a generalist insect using more than 50 plant species in at least nine genera throughout its large geographical range (Johnson and Kingsolver 1976; Johnson et al. 1989; Nilsson and Johnson 1993). Host-associated life-history plasticity, including egg size plasticity, may allow the exploitation of numerous host species. Alternatively, the generalist life history of this beetle may promote the evolution of phenotypic plasticity. These hypotheses are currently under investigation in our lab.

LITERATURE CITED

Avelar, T. 1993. Egg size in *Drosophila:* standard unit of investment or variable response to environment? the effect of temperature. Journal of Insect Physiology 39:283–289.

Bagenal, T. B. 1971. The interrelation of the size of fish eggs, the date of spawning, and the production cycle. Journal of Fisheries Biology 3:207–219.

Baur, B. 1990. Seasonal changes in clutch size, egg size, and mode of oviposition in *Arianta arbustorum* L. (Gastropoda) from alpine populations. Zoologsiche Anzeitschrift 225:253–264.

Beacham, T. D., and C. B. Murray. 1993. Fecundity and egg size variation in North American Pacific salmon (*Oncorhynchus*). Journal of Fisheries Biology 42:485–508.

Berrigan, D. 1991. The allometry of egg size and number in insects. Oikos 60:313–321.

Braby, M. F. 1994. The significance of egg size variation in butterflies in relation to host plant quality. Oikos 71:119–129.

Danks, H. V. 1987. Insect dormancy: an ecological perspective. Biological Survey of Canada, National Museum of Natural Sciences, Ottawa.

Devauchelle, N., J. C. Alexandre, N. LeCorre, and Y. Letty. 1987. Spawning of sole (*Solea solea*) in captivity. Aquaculture 66:125–147.

Fleming, I. A., and M. T. Gross. 1990. Latitudinal clines: a trade-off between egg number and size in pacific salmon. Ecology 71:1–11.

Fox, C. W. 1993. The influence of maternal age and mating frequency on egg size and offspring performance in *Callosobruchus maculatus* (Coleoptera: Bruchidae). Oecologia (Berlin) 96: 139–146.

———. 1994a. The influence of egg size on offspring performance in the seed beetle, *Callosobruchus maculatus*. Oikos 71:321–325.

———. 1994b. Maternal and genetic effects on egg size and larval performance in the seed beetle, *Callosobruchus maculatus*. Heredity 73:509–517.

Fox, C. W., and H. Dingle. 1994. Dietary mediation of maternal age effects on offspring performance in a seed beetle (Coleoptera: Bruchidae). Functional Ecology 8:600–606.

Fox, C. W., and T. A. Mousseau. 1996. Larval host plant affects the fitness consequences of egg size in the seed beetle *Stator limbatus*. Oecologia (Berlin) 107:541–548.

Fox, C. W., K. J. Waddell, and T. A. Mousseau. 1994. Host-associated fitness variation in a seed beetle (Coleoptera: Bruchidae): evidence for local adaptation to a poor quality host. Oecologia (Berlin) 99:329–336.

Fox, C. W., L. A. McLennan, and T. A. Mousseau. 1995a. Male body size affects female lifetime reproductive success in a seed beetle. Animal Behaviour 50:281–284.

Fox, C. W., K. J. Waddell, and T. A. Mousseau. 1995b. Parental host plant affects offspring life histories in a seed beetle. Ecology 76:402–411.

Fox, L. R., and P. A. Morrow. 1981. Specialization: species property or local phenomenon? Science (Washington, D.C.) 211:887–893.

Garcia-Barros, E. 1992. Evidence for geographic variation of egg size and fecundity in a satyrine butterfly, *Hipparchia semele* (L.) (Lepidoptera, Nymphalidae-Satyrinae). Grasellsia 48:45–52.

———. 1994. Egg size variation in European satyrine butterflies (Nymphalidae, Satyrinae). Biological Journal of the Linnean Society 51:309–324.

Guisande, C., and Z. M. Gliwicz. 1992. Egg size and clutch size in two *Daphnia* species grown at different food levels. Journal of Plankton Research 14:997–1007.

Harvey, G. T. 1983. A geographical cline in egg weights in *Choristoneura fumiferana* (Lepidoptera: Tortricidae) and its significance in population dynamics. Canadian Entomologist 115: 1103–1108.

Janzen, D. H. 1977. Variation in seed size within a crop of a Costa Rican *Micuna andreana* (Leguminosae). American Journal of Botany 64:347–349.

Johnson, C. D., and J. M. Kingsolver. 1976. Systematics of *Stator* of North and Central America (Coleoptera: Bruchidae). U.S. Department of Agriculture Technical Bulletin 1537:1–101.

Johnson, C. D., J. M. Kingsolver, and A. L. Teran. 1989. Sistematica del genero *Stator* (Insecta: Coleoptera: Bruchidae) en Sudamerica. Opera Lilloana 37:1–105.

Kaplan, R. H. 1991. Developmental plasticity and maternal effects in amphibian life histories. Pages 794–799 *in* E. C. Dudley, ed. The unity of evolutionary biology. Vol. 2. Dioscoridies, Portland, Oreg.

Kawecki, T. J. 1995. Adaptive plasticity of egg size in response to competition in the cowpea weevil, *Callosobruchus maculatus* (Coleoptera: Bruchidae). Oecologia (Berlin) 102:81–85.

Lacey, E. P. 1991. Parental effects on life-history traits in plants. Pages 735–744 *in* E. C. Dudley, ed. The unity of evolutionary biology. Vol. 2. Dioscoridies, Portland, Oreg.

Mashiko, K. 1992. Genetic egg and clutch size variations in freshwater prawn populations. Oikos 63: 454–458.

McGinley, M. A., D. H. Temme, and M. A. Geber. 1987. Parental investment in offspring in variable environments: theoretical and empirical considerations. American Naturalist 130:370–398.

Miller, J. M., J. S. Burke, and G. R. Fitzhugh. 1991. Early life history patterns of Atlantic North

American flatfish: likely (and unlikely) factors controlling recruitment. Netherlands Journal of Sea Research 27:261–275.

Mousseau, T. A., and H. Dingle. 1991a. Maternal effects in insect life histories. Annual Review of Entomology 36:511–534.

———. 1991b. Maternal effects in insects: examples, constraints, and geographic variation. Pages 745–761 in E. C. Dudley, ed. The unity of evolutionary biology. Vol. 2. Dioscoridies, Portland, Oreg.

Nilsson, J. A., and C. D. Johnson. 1993. Laboratory hybridization of Stator beali and S. limbatus, with new host records for S. limbatus and Mimosestes amicus (Coleoptera: Bruchidae). Southwestern Naturalist 38:385–387.

Parker, G. A., and M. Begon. 1986. Optimal egg size and clutch size: effects of environment and maternal phenotype. American Naturalist 128:573–592.

Perrin, N. 1989. Population density and offspring size in the cladoceran Simocephalus vetulus (Muller.). Functional Ecology 3:29–36.

Platenkamp, G. A. J., and R. G. Shaw. 1993. Environmental and genetic maternal effects on seed characters in Nemophila menziesii. Evolution 47:540–555.

Reznick, D. N. 1991. Maternal effects in fish life histories. Pages 78–93 in E. C. Dudley, ed. The unity of evolutionary biology. Vol. 2. Dioscoridies, Portland, Oreg.

Rijnsdorp, A. D., and B. Vingerhoed. 1994. The ecological significance of geographical and seasonal variation in egg size in sole Solea solea (L.). Netherlands Journal of Sea Research 32: 255–270.

Riska, B. 1991. Introduction to the symposium. Pages 719–724 in E. C. Dudley, ed. The unity of evolutionary biology. Vol. 2. Dioscoridies, Portland, Oreg.

Roach, D. A., and R. Wulff. 1987. Maternal effects in plants: evidence and ecological and evolutionary significance. Annual Review of Ecology and Systematics 18:209–235.

Rounsefell, G. A. 1957. Fecundity of North American salmonidae. U.S. Fish and Wildlife Service Fisheries Bulletin 57:451–467.

Rowe, J. W. 1994. Reproductive variation and the egg size–clutch size trade-off within and among populations of painted turtles (Chrysemys picta bellii). Oecologia (Berlin) 99:35–44.

SAS. 1985. SAS user's guide: statistics. Version 5.0 ed. SAS Institute, Cary, N.C.

Saunders, D. S. 1982. Insect clocks. 2d ed. Pergamon, Oxford.

Sibly, R. M., and P. Calow. 1983. An integrated approach to life-cycle evolution using selective landscapes. Journal of Theoretical Biology 102:527–547.

Siemens, D. H., and C. D. Johnson. 1990. Host-associated differences in fitness within and between populations of a seed beetle (Bruchidae): effects of plant variability. Oecologia (Berlin) 82: 408–423.

Siemens, D. H., C. D. Johnson, and R. L. Woodman. 1991. Determinants of host range in bruchid beetles. Ecology 72:1560–1566.

Siemens, D. H., C. D. Johnson, and K. V. Ribardo. 1992. Alternative seed defense mechanisms in congeneric plants. Ecology 73:2152–2166.

Sinervo, B. 1991. Experimental and comparative analyses of egg size in lizards: constraints on the adaptive evolution of maternal investment per offspring. Pages 725–734 in E. C. Dudley, ed. The unity of evolutionary biology. Vol. 2. Dioscoridies, Portland, Oreg.

Singer, M. C. 1986. The definition and measurement of oviposition preference in plant-feeding insects. Pages 65–94 in J. Miller and T. A. Miller, eds. Insect-plant relations. Springer, New York.

Smith, C. C., and S. D. Fretwell. 1974. The optimal balance between size and number of offspring. American Naturalist 108:499–506.

Smith, F. E. 1963. Population dynamics in Daphnia magna and a new model for population growth. Ecology 44:651–663.

Wasserman, S. S. 1986. Genetic variation in adaptation to foodplants among populations of the southern cowpea weevil, Callosobruchus maculatus: evolution of oviposition preference. Entomologia Experimentalis et Applicata 42:201–212.

Associate Editor: Nancy A. Moran