

# Genetic and Maternal Influences on Body Size and Development Time in the Seed Beetle *Stator limbatus* (Coleoptera: Bruchidae)

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**ABSTRACT** I investigated the relative contributions of genetic and maternal effects to variation in body size and egg-to-development time in 4 populations of the seed beetle *Stator limbatus* (Horn), using parent-offspring relationships and a half-sib experiment. Most estimates of the heritability of body size were significantly greater than zero (range was 0.21-0.72, depending on progeny sex and the population). However, there was little evidence of genetic variation in development time in any population. Instead, development time was influenced largely by maternal effects, consistent with the interpretation of previous experiments that larvae adjust the length of their development period to compensate for variation among their mothers. Estimates of genetic and phenotypic covariances between body size and development time were all negative, suggesting that genetic variation in general vigor is present within populations.

**KEY WORDS** *Stator limbatus*, genetic variation, heritability, maternal effect, quantitative genetics

BODY SIZE IS generally under directional or balancing selection in nature. In the seed beetle *Stator limbatus* (Horn), sexual selection favors the evolution of large males—females mating to small males remate more readily than females mating to large males (Savalli and Fox 1997). Likewise, fecundity selection favors the evolution of large females because they lay more eggs than small females (Fox et al. 1995a, 1997a). However, the response of body size to natural selection depends on the magnitude of selection, the amount of genetic variation present within populations, genetic correlations between body size and other characters (such as development time), and the magnitude of selection on those characters. Thus, one objective of the following study was to quantify the amount of additive genetic variation in body size and development time, and the genetic correlation between them, in populations of *S. limbatus*.

Although long-term evolutionary responses to natural selection are largely determined by genetic variation, genetic correlations, and the magnitude of selection, some sources of environmental variation can influence short-term evolutionary responses to selection. Maternal effects—nongenetic effects of maternal phenotype or environment on progeny phenotype (Falconer 1965, Mousseau and Dingle 1991, Mousseau and Fox 1997, Wade 1997)—provide a mechanism for the inheritance of nongenetic variation (Fox and Savalli 1997). They can result in large time lags in responses to selection, and characters subject to large maternal effects may even respond to selection in a maladaptive direction (Riska et al. 1985, Kirkpatrick and Lande 1989, Lande and Kirk-

patrick 1990). In animals, we generally observe maternal effects on early development of progeny, but rarely on final adult characteristics, such as size at maturation (Bernardo 1996). This is because progeny can be developmentally plastic, compensating for maternal effects by modifying development. For example, progeny may extend development time to compensate for small egg size (Fox 1993, 1994). However, maternal effects have been shown to affect progeny adult characters in some animals, such as the seed beetle *Callosobruchus maculatus* (F.), in which offspring cannot compensate adequately for the environmental variation caused by maternal food stress (e.g., Fox and Savalli 1997). Thus, examination of the magnitude and form of maternal effects on characters such as body size and development time is critical to understanding the evolution of these characters.

Here, I investigate the relative contributions of genetic and maternal effects to variation in body size and development time in the seed beetle *S. limbatus*. I find that body size variation is heritable, but that egg-to-adult development time is influenced more by maternal effects than by genetic variation. Consistent with previously published results, this indicates that progeny can compensate for variation in egg quality among their mothers by varying their development period as needed to emerge at a genetically targeted body size.

## Materials and Methods

**Natural History of *S. limbatus*.** *S. 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, Johnson 1995). Throughout its large geographic range, *S. limbatus* has been reared from seeds of >70 plant species in at least 9 genera (this increase over previous reports of the number of species that *S. limbatus* feeds on results from the conclusion of Johnson [1995] of synonymy of *S. limbatus* and *S. ceareanus*). In the United States, and particularly in Arizona, it is abundant on many species of *Acacia* (Fabaceae: Mimosoideae) and 2 species of *Cercidium* (*C. floridum* and *C. microphyllum*; paloverdes; Fabaceae: Caesalpinioideae), although only one or a few hosts may be available in any single locality. Two other hosts, *Parkinsonia aculeata* L. and *Chloroleucon ebano* (Berlandier), have been introduced into central Arizona for ornamental purposes, and their seeds are oviposited upon by *S. limbatus*. However, even where they escaped from cultivation these plants are uncommon and *S. limbatus* larval survivorship is very low on their seeds (e.g., Fox et al. 1996, 1997b), such that they are ecologically relatively unimportant hosts in nature.

Females oviposit directly onto host seeds primarily inside fruits that have either begun dehiscence or been damaged by other organisms. Upon hatching, the larvae burrow into the seed, where they complete development and pupate. They emerge from seeds as adults. Adults are the only dispersing stage; larvae are restricted to the seed that their mother has chosen for them. In the laboratory, mating and egg laying begin  $\approx 24$ –48 h after emergence. Beetles require only the resources inside a single seed to complete development and reproduce. Thus, neither food nor water supplementation were necessary for the following laboratory experiments.

Further details on the ecology and behavior of these beetles can be found in Fox et al. (1994, 1995b), Savalli and Fox (1997), Siemens and Johnson (1990, 1992), and Siemens et al. (1991, 1992).

**Study Populations.** Two separate experiments were conducted at different times, using different populations of beetles. For the 1st experiment, beetles were collected from 2 localities in central Arizona. On 5–6 September 1993, beetles were collected from *Cercidium floridum* (Fabaceae: Caesalpinioideae) along Scottsdale Highway, 2 km north of Bell Road (behind the Scottsdale Well), in Scottsdale, Maricopa County, Arizona (Scottsdale population) ( $\approx 33^{\circ} 41' N$ ,  $111^{\circ} 53' W$ ). On 7 September 1993, beetles were collected from *Acacia greggii* (Fabaceae: Mimosoideae) in numerous locations throughout Black Canyon City, Yavapai County, Arizona (Black Canyon City population) ( $\approx 34^{\circ} 05' N$ ,  $112^{\circ} 07' W$ ). These 2 populations are  $\approx 50$  km apart and differ in the host plants available to them. In Black Canyon City, *A. greggii*, *C. floridum*, and *C. microphyllum* are each abundant, and all are attacked by *S. limbatus* (personal observation). In Scottsdale, *C. floridum* is abundant and *C. microphyllum* and *A. greggii* are uncommon or rare.

For the 2nd experiment, beetles were collected from 1 population in central Arizona and 1 in western Texas. On 25 June 1995, beetles were collected from *Acacia berlandieri* (Fabaceae: Mimosoideae) along Highway 277,  $\approx 15$  km south of Del Rio, Val Verde County, Texas (Del Rio population) (the area around  $29^{\circ} 19' N$ ,  $100^{\circ} 48' W$ ). On 20 August 1995, beetles were collected from *Cercidium floridum* and *C. microphyllum* along Mountainview Road in Apache Junction, Pinal County, Arizona (Apache Junction Population) ( $\approx 33^{\circ} 25' N$ ,  $111^{\circ} 27' W$ ).

Beetles and seed stock were collected by picking mature seed pods from >25 plants at each site. Mature pods were transferred to the laboratory and seeds bearing beetle eggs were separated from uninfested seeds. Seeds containing entrance or emergence holes of other bruchids (such as *Mimosestes* sp.) were discarded. I estimate that all laboratory populations were initiated with at least 200 field-collected individuals. The populations were reared in the laboratory for 2 (Scottsdale, Black Canyon City, and Apache Junction populations) or 4 (Del Rio population) generations, on either seeds of the host from which they were collected or seeds of *A. greggii*, before the experiments were initiated. To minimize the effect of selection occurring during the experiment on heritability estimates, all beetles (parents and progeny) were reared on seeds of *A. greggii* because larval mortality is very low on this species.

**Experimental Design.** To estimate the heritability of adult body mass and egg-to-adult development time, I conducted 2 experiments using different populations of beetles. In the 1st experiment, I estimated the heritability of body size and development time from the relationship between parents and their offspring (Falconer 1989). This experiment was executed simultaneously on both the Apache Junction and Scottsdale populations.

Within 24 h of emerging as an adult, virgin females, reared on seeds of *A. greggii* at low density (1 larva per seed), were each weighed and then paired with a single virgin male (from the same population) that had likewise been reared at low density on seeds of *A. greggii* ( $N = 80$  and  $69$  for the Black Canyon City and Scottsdale populations, respectively). Pairs were confined in 35-mm petri dishes with 10 seeds of *A. greggii* and allowed to lay eggs. Dishes were checked for eggs at 12-h intervals. Seeds bearing eggs were replaced with clean seeds until a female laid 10 or more eggs. All offspring were reared to adult at a density of 1 larva per seed,  $28^{\circ}C$ , 24 h light. Emerging adults were collected and individually weighed (to 0.1 mg precision) within 12 h of adult emergence. Development time was estimated as the time between egg-laying and adult emergence and thus includes embryonic, larval, and pupal development times.

From this 1st experiment, I estimated the heritability of male body size and development time by regressing the average body mass or development time of all male progeny for each family against the

Table 1. Heritability estimates of adult body mass and development time of *S. limbatus* based on parent-offspring regressions in experiment 1

Character/Population	Females	Males
Adult Body Mass		
Black Canyon City	0.30 ± 0.20 (72)NS	0.32 ± 0.14 (79)*
Scottsdale	0.22 ± 0.16 (69)NS	0.72 ± 0.20 (61)***
Egg-to-adult Development Time		
Black Canyon City	0.30 ± 0.34 (72)NS	0.0 ± 0.72 (80)NS
Scottsdale	0.40 ± 0.30 (69)NS	0.0 ± 0.28 (62)NS

Means ± SEM (number of families). \*,  $P < 0.05$ ; \*\*\*,  $P < 0.001$ ; NS, nonsignificant.

body mass or development time of fathers (i.e., the mean size or development time of each family was treated as single data in the regression analyses). The heritability of female body size and development time was estimated by regressing the average body mass or development time of all female progeny for each family against the body mass or development time of mothers. Because the beetles are sexually dimorphic in both body size and development time, a combined analysis was not performed.

In the 2nd experiment, I used a traditional half-sib design (Falconer 1989) to estimate genetic variation in adult body mass and egg-to-adult development time. This experiment was executed using the Del Rio and Apache Junction populations. To create half-sib families, virgin male beetles (59 sires in the Del Rio population and 61 in the Apache Junction population) were each mated sequentially to between 2 and 4 different virgin females, creating 189 and 168 full-sib families (Del Rio and Apache Junction, respectively). Each virgin male, collected within 12 h of his emergence from an isolated host seed, was confined with a virgin female (likewise collected <12 h after emergence) in a 35-mm petri dish containing 12 *A. greggii* seeds and allowed to copulate. Pairs were confined until the female laid at least 1 egg, after which the male was transferred to another 35-mm dish containing a different virgin female and again confined until his mate laid at least 1 egg. This procedure was repeated until males successfully fertilized 4 females, or died. Dishes containing egg-laying females were checked for eggs at 24-h intervals. Seeds bearing eggs were replaced with clean seeds until a female had laid eggs on  $\geq 10$  seeds.

All eggs were reared to adult on *A. greggii* seeds at densities of 1 beetle per seed (excess eggs were scraped off), 29°C, and a photoperiod of 15:9 (L:D) h. Egg-to-adult development time and body mass at adult emergence were recorded for all offspring, as in the 1st experiment. In total, 1,633 females and 1,668 males were reared to adult from the Del Rio population, and 1,263 females and 1,310 males were reared from the Apache Junction population.

### Results

The parent-offspring regression analyses from the 1st experiment indicate that the heritability of male body mass was significantly greater than zero

in both the Black Canyon City and Scottsdale populations ( $h^2 = 0.32 \pm 0.14$  and  $0.72 \pm 0.20$ , respectively; Table 1). The estimate of  $h^2$  of female body mass was also positive, but it was not significantly different from zero for either population. The estimates of  $h^2$  for egg-to-adult development time did not differ from zero for either sex in either population (Table 1), suggesting that there is either little or no additive genetic variation for this character in these 2 populations, or that the amount of additive genetic variation within the populations is small relative to environmental sources of variation. However, the regression analyses suggest that maternal effects may influence development time. Some of the maternal effects variance is contained in the mother-daughter estimate of  $h^2$  (how much depends on the type of maternal effect), whereas none is contained in the father-son estimate of  $h^2$ . Although not differing statistically from zero, the mother-daughter estimates of  $h^2$  for development time were much larger than the father-son estimates, which were both zero (Table 1).

In the 2nd experiment, an analysis of variance (ANOVA) detected large sire and dam (nested within sire) effects on offspring adult body mass in both the Del Rio and Apache Junction populations (Table 2). The large sire effects translated into nonzero estimates of additive genetic variation ( $V_A$ ) for adult body mass, and heritabilities of between 0.21 and 0.43 (i.e., additive genetic effects explained 21–43% of the phenotypic variance; Table 2). Maternal effects had little influence on progeny adult body mass—the largest estimated proportion of the phenotypic variance explained by maternal effects was 7.8% (average was 4.0%), substantially less than the proportion explained by additive genetic effects (Table 2).

As in the 1st experiment, there was no evidence from the 2nd experiment that development time was heritable in either the Del Rio or Apache Junction populations (Table 3). Although an ANOVA detected a highly significant effect of dam (nested within sire) on development time (i.e., a large effect of mothers), there was no effect of sire (father) in either population. These nonsignificant sire effects translated into very small heritability estimates (ranging from 0 to 0.10), none of which differed significantly from zero. The large dam effects, however, translated into estimated maternal effects explaining between 7.5 and 20.1% of the phenotypic

Table 2. Nested ANOVA and estimated variance components for adult body mass of *S. limbatus*

Source	R <sup>2</sup>	ANOVA			Variance components ( $\times 10^{-1}$ )		
		df	MS	F	Observational	Genetic	
Apache Junction population							
Female progeny							
Site		60	0.673	1.75**	V <sub>S</sub> = 0.177	V <sub>A</sub> = 0.707	31.6 ± 13.5%
Dam (sire)		101	0.385	2.17***	V <sub>D</sub> = 0.287	V <sub>M</sub> = 0.110	4.9%
Error		1,091	0.177		V <sub>E</sub> = 1.773	V <sub>e</sub> = 1.420	63.5%
	0.30				V <sub>P</sub> = 2.237		
Male progeny							
Sire		60	0.867	2.25***	V <sub>S</sub> = 0.290	V <sub>A</sub> = 1.158	42.9 ± 13.1%
Dam (sire)		105	0.386	1.77***	V <sub>D</sub> = 0.244	V <sub>M</sub> = 0	0%
Error		1,130	0.218		V <sub>E</sub> = 2.168	V <sub>e</sub> = 1.544	57.1%
	0.30				V <sub>P</sub> = 2.702		
Del Rio population							
Female progeny							
Sire		58	0.948	1.73**	V <sub>S</sub> = 0.165	V <sub>A</sub> = 0.661	24.5 ± 10.2%
Dam (sire)		122	0.549	2.53***	V <sub>D</sub> = 0.377	V <sub>M</sub> = 0.212	7.8%
Error		1,436	0.217		V <sub>E</sub> = 2.160	V <sub>e</sub> = 1.829	67.7%
	0.29				V <sub>P</sub> = 2.702		
Male progeny							
Sire		58	0.917	1.76**	V <sub>S</sub> = 0.171	V <sub>A</sub> = 0.686	21.1 ± 8.5%
Dam (sire)		125	0.522	1.86***	V <sub>D</sub> = 0.283	V <sub>M</sub> = 0.112	3.4%
Error		1,467	0.280		V <sub>E</sub> = 2.798	V <sub>e</sub> = 2.454	75.5%
	0.24				V <sub>P</sub> = 3.252		

Type III sums of squares were calculated using SAS general linear models procedure (SAS Institute 1985; PROC GLM). Variance components were estimated using the restricted maximum likelihood method of SAS VARCOMP. The maternal effects variance (V<sub>M</sub>) was calculated assuming that the dominance variance and higher order interactions (e.g., V<sub>AA</sub>, V<sub>AAA</sub>) were 0. Standard errors for the percentage of V<sub>P</sub> explained by V<sub>A</sub> (=h<sup>2</sup>) were calculated following Becker (1992). V<sub>S</sub>, among sire variance component; V<sub>D</sub>, among dam variance component; V<sub>E</sub>, error variance in ANOVA; V<sub>P</sub>, total phenotypic variance; V<sub>A</sub>, additive genetic variance; V<sub>M</sub>, maternal variance; V<sub>e</sub>, environmental variance. \*\*, P < 0.01; \*\*\*, P < 0.001.

variance in development time. This latter result is consistent with the observation from the 1st experiment that the mother-daughter estimates of h<sup>2</sup> for development time were larger than the father-son estimate.

Although my estimates of the additive genetic variance in development time are near (or at) zero for both sexes in each population, it is unlikely that

there is an absence of genetic variation in development time in either population—estimates of the additive genetic covariance between body size and development time {estimated from the relationship  $\text{cov}(X,Y) = [\text{var}(X+Y) - \text{var}(X) - \text{var}(Y)]/2$ } were between -0.354 and -0.241 for each population and sex. It was not possible to calculate additive genetic correlations because some of the additive

Table 3. Nested ANOVA and estimated variance components for egg-to-adult development time of *S. limbatus*

Source	R <sup>2</sup>	ANOVA			Variance components ( $\times 10^{-1}$ )		
		df	MS	F	Observational	Genetic	
Apache Junction population							
Female progeny							
Site		60	7.66	0.74NS	V <sub>S</sub> = 0	V <sub>A</sub> = 0	0%
Dam (sire)		101	10.40	2.90***	V <sub>D</sub> = 0.710	V <sub>M</sub> = 0.710	16.3%
Error		1,099	3.58		V <sub>E</sub> = 3.654	V <sub>e</sub> = 3.654	83.7%
	0.27				V <sub>P</sub> = 4.364		
Male progeny							
Sire		60	10.68	0.93NS	V <sub>S</sub> = 0.039	V <sub>A</sub> = 0.158	3.4 ± 11.0%
Dam (sire)		105	11.43	3.18***	V <sub>D</sub> = 0.975	V <sub>M</sub> = 0.936	20.1%
Error		1,142	3.60		V <sub>E</sub> = 3.652	V <sub>e</sub> = 3.572	76.6%
	0.31				V <sub>P</sub> = 4.666		
Del Rio population							
Female progeny							
Sire		58	10.28	1.29NS	V <sub>S</sub> = 0.109	V <sub>A</sub> = 0.437	10.2 ± 7.1%
Dam (sire)		122	7.95	2.14***	V <sub>D</sub> = 0.432	V <sub>M</sub> = 0.323	7.5%
Error		1,449	3.72		V <sub>E</sub> = 3.754	V <sub>e</sub> = 3.535	82.3%
	0.23				V <sub>P</sub> = 4.295		
Male progeny							
Sire		58	7.31	0.89NS	V <sub>S</sub> = 0	V <sub>A</sub> = 0	0%
Dam (sire)		125	8.24	2.01***	V <sub>D</sub> = 0.422	V <sub>M</sub> = 0.422	9.3%
Error		1,478	4.09		V <sub>E</sub> = 4.110	V <sub>e</sub> = 4.110	90.7%
	0.24				V <sub>P</sub> = 4.532		

Footnote as in Table 2. \*\*\*, P < 0.001; NS, P > 0.05.

genetic variance estimates were zero (see Table 3). Although the additive genetic covariances are low relative to the magnitude of the additive genetic variance, that they are consistent in sign and magnitude suggests that the additive genetic variance in development time is not zero—the covariances should be zero if the additive genetic variance in either body size or development time was zero. The phenotypic covariances and correlations were likewise all negative, ranging from  $-1.76$  to  $-1.12$  and from  $-0.459$  to  $-0.357$  ( $P < 0.01$  for each,  $N = 59$  to  $61$  families for each), respectively.

### Discussion

My results indicate that body size is heritable in *S. limbatus*, but that egg-to-adult development time is influenced more by maternal effects than by genetic variation. This is consistent with previous experiments on *S. limbatus* (Fox 1997a, b) in which I found that, although egg size varies substantially among females, progeny can compensate for some of this variation by extending development. For example, mothers reared at high density lay smaller eggs than mothers reared at low density, but their progeny compensate for this by extending development to attain what appears to be a genetically targeted body size (Fox 1997a). The results from my parent-offspring and half-sib experiments likewise indicate that variation among females does not affect the body size of their offspring independent of the genes that mothers pass to progeny. Instead, body size is largely genetically targeted. The large maternal effect on development time is consistent with the interpretation of previous experiments that larvae adjust the length of their development period to compensate for variation among their mothers.

Similar results are generally found in other egg-laying animals without parental care. With the notable exceptions of maternal control of progeny diapause, flight polymorphisms, and sexual versus asexual reproduction in some animals (reviewed in Fox and Mousseau 1997), maternal effects are rarely detectable in adult progeny. Instead, progeny tend to be developmentally plastic, compensating for maternal effects in early development. For example, in another seed beetle, *Callosobruchus maculatus* (F.), eggs laid by older mothers are smaller than eggs laid by younger mothers, but larvae compensate for small egg size by extending development (Fox 1993, Fox and Dingle 1994). Also, using half-sib designs similar to that employed here, both Kawecki (1995) and I (Fox 1994) found high heritabilities for body size of *C. maculatus*, but low heritabilities and large maternal effects for development time. However, progeny of *C. maculatus* mothers reared at high density (20 larvae per seed) emerge smaller than progeny of mothers reared at low density (1 egg per seed), demonstrating that nongenetic variation among mothers can affect the adult body size of their progeny (Fox and Savalli 1997).

Interestingly, my estimates of the heritability of body mass in *S. limbatus* are lower than is generally reported for body size in other seed beetles. For example, estimates of the heritability of body size for *C. maculatus* range from 0.50 to 0.90 (Miller et al. 1989, Messina 1993, Fox 1994), although Kawecki (1995) found that heritabilities of body size were consistently lower when *C. maculatus* was reared on a novel host plant. It is unlikely that my estimates reflect genetic bottlenecks when the beetles were brought into the laboratory, because each laboratory population was established with  $>200$  individuals. The beetles were only reared in the laboratory for 2–4 generations before the start of the genetic experiments, and their populations were allowed to expand in size during this time, so a reduction in genetic variation associated with intense selection in the laboratory is also unlikely. Thus, the low heritabilities probably reflect either inflated phenotypic variation associated with bringing the beetles into a novel environment (the laboratory), decreased additive genetic variation expressed in the novel environment (as observed by Kawecki 1995), or low heritabilities in nature. Regardless of why the heritability of *S. limbatus* body size is smaller in magnitude than generally observed, however, body size is heritable and should be capable of responding to the natural selection that appears to be operating in nature (Fox et al. 1995a, Savalli and Fox 1997). For development time, however, I found little genetic variation in any of the populations examined, which is consistent with the generally low heritabilities estimated for development time in many other insects (Miyatake 1995) including other seed beetles (Fox 1994, Kawecki 1995). This indicates that selection on development time should produce at most a very slow evolutionary response in *S. limbatus*.

Although my estimates of the genetic and maternal effects variances were generally consistent with my expectations, the negative phenotypic and genetic covariances between body mass and development time are opposite in sign from those generally reported in the literature (review in Miyatake 1995). Longer development period is generally associated with larger adult size, resulting in positive phenotypic and genetic correlations between them (Robertson 1960, 1963; Tanaka 1989; Partridge and Fowler 1993; Fox 1994, Miyatake 1995; but see Møller et al. 1989). For *S. limbatus*, longer development time was associated with smaller adult body size, suggesting phenotypic and genetic variation in overall vigor (Futuyma and Philippi 1987, Jaenike 1990) or feeding rate (Burnet et al. 1977). In fact, negative correlations between body size and development time are predicted by life-history theory when there is variation in growth rate within populations (Roff 1992, Stearns 1992). A genotype  $\times$  laboratory environment interaction within my laboratory populations could also result in negative covariances between body size and development time if some genotypes generally performed well in

the laboratory environment (developing fast and emerging large), whereas other genotypes did not. This relationship between body size and development time will be the subject of future research in my laboratory.

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