

- tica*). IV. Patterns of fluctuating asymmetry and selection against asymmetry. *Evolution* 48:658–670.
- MØLLER, A. P., AND A. POMIANKOWSKI. 1994. Fluctuating asymmetry and sexual selection. Pp. 269–281 in T. A. Markow, ed. *Developmental instability: its origins and evolutionary implications*. Kluwer Academic Publishers, Dordrecht, The Netherlands.
- MULVEY, M. G., P. KELLER, AND G. K. MEFFE. 1994. Single- and multiple-locus genotypes and life-history responses of *Gambusia holbrooki* reared at two temperatures. *Evolution* 48:1810–1819.
- PALMER, A. R. 1994. Fluctuating asymmetry analyses: a primer. Pp. 355–564 in T. A. Markow, ed. *Developmental instability: its origins and evolutionary implications*. Kluwer Academic Publishers, Dordrecht, The Netherlands.
- PALMER, A. R., AND C. STROBECK. 1992. Fluctuating asymmetry as a measure of developmental stability: implications of non-normal distributions and power of statistical tests. *Acta Zool. Fennica* 191:57–72.
- PALMER, A. R., C. STROBECK, AND A. K. CHIPPINDALE. 1994. Bilateral variation and the evolutionary origin of macroscopic asymmetries. Pp. 201–218 in T. A. Markow, ed. *Developmental instability: its origins and evolutionary implications*. Kluwer Academic Publishers, Dordrecht, The Netherlands.
- PARSONS, P. A. 1990. Fluctuating asymmetry: an epigenetic measure of stress. *Biol. Rev. (Cambridge)* 65:131–145.
- RICE, W. R. 1989. Analyzing tables of statistical tests. *Evolution* 43:223–225.
- SMITH, L. H. 1994. Fluctuating asymmetry and developmental stability in Cambrian and Ordovician trilobites. *GSA Abstract with Programs* 27:A373.
- SOKAL, R. R., AND F. J. ROHLF. 1981. *Biometry*. 2d ed. Freeman, New York.
- STRATHMANN, M. F. 1987. *Reproduction and development of marine invertebrates of the northern Pacific Coast. Data and methods for the study of eggs, embryos, and larvae*. Univ. of Washington Press, Seattle.
- STRATHMANN, R. R., L. FENAUX, AND M. F. STRATHMANN. 1992. Heterochronic developmental plasticity in larval sea urchins and its implications for evolution of nonfeeding larvae. *Evolution* 46:972–986.
- WATSON, P. J., AND R. THORNHILL. 1993. Fluctuating asymmetry and sexual selection. *Trends Ecol. Evol.* 9:21–25.

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THE ECOLOGY OF BODY SIZE IN A SEED BEETLE, *STATOR LIMBATUS*: PERSISTENCE OF ENVIRONMENTAL VARIATION ACROSS GENERATIONS?

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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 progeny phenotype, independent of progeny genotype (Mousseau and Dingle 1991; Riska 1991). Thus, maternal effects provide a nongenetic mechanism by which environmental variation in the parental generation affects the phenotype of their progeny (Riska et al. 1985). However, maternal effects are generally only studied for a single generation, and often only at early developmental stages of progeny. Surprisingly few studies have examined how long maternal effects persist within populations (Bernardo 1996a), and those that have done this typically examine the persistence of environmental variation in nonstressed populations (e.g., Fox 1994a). These few studies suggest that although maternal effects often have large effects on progeny phenotype early in ontogeny, they are often undetectable later in ontogeny (Roach and Wulff 1987; Mousseau and Dingle 1991; Mousseau and Fox, in press), presumably due to compensatory growth by progeny.

In animals, body size is an important maternal character that affects offspring phenotypes because maternal size generally affects egg size and/or composition, which in turn can affect progeny growth and development, and possibly even progeny size at reproduction (reviews in Fleming and Gross 1990; Kaplan 1991; Reznick 1991; Fox 1994b; Bernardo 1996b; Fox and Mousseau 1996). Thus, environmental variation affecting egg production in the grandparental generation may affect an animal's body size—environmental variation affects female size, and thus the size of her propagules, which in turn can affect offspring size, and thus the size of their propagules, and so on. As a result, nongenetic variation in maternal body size might be transmitted across multiple generations (Falconer 1965).

In the seed beetle *Stator limbatus* (Coleoptera: Bruchidae), there is substantial variation in body size both within and among populations. Much of this variation is due to resource competition among larvae in nature. *Stator limbatus* females lay their eggs on seeds of their host plants, and larvae subsequently complete larval development inside the seed selected by their mothers, emerging only after pupation. Thus,

these larvae develop on discrete resource patches. In nature, seeds of *S. limbatus* host plants appear to be a limiting resource (Fox et al. 1996), so that most seeds must support multiple larvae. Due to intense larval competition within seeds (Siemens et al. 1992; Fox et al. 1996), beetles developing from seeds bearing more eggs emerge at much lower body weight than beetles developing from seeds bearing fewer eggs—large beetles from low-density seeds and small beetles from high-density seeds can differ in body weight by more than an order of magnitude (Fox et al. 1996). These smaller females lay, on average, smaller eggs than larger females (Fox et al. 1995a), which could subsequently produce smaller adult progeny. Thus, body size variation resulting from larval competition may persist for many generations in a population, even when resource competition is no longer a factor.

Here I test the hypothesis that the substantial nongenetic body size variation generated by resource competition among larvae of *S. limbatus* persists in the population for multiple generations after resource competition has been relaxed. Density-induced body size variation in *S. limbatus* provides an excellent opportunity to demonstrate the persistence of nongenetic body size variation across generations because body size varies by over an order of magnitude, and survivorship of beetles is very high at any density on some host plants (Fox et al. 1996), such that selection on body size can be largely eliminated during experiments. I find that environmentally induced body size variation does not persist across generations in *S. limbatus*. Instead, although beetles reared at high density are substantially smaller than beetles reared at lower density, these females lay eggs that are only slightly smaller (3–5%) than those laid by females reared at lower density, and progeny developing from these smaller eggs develop longer (0.5–0.8 d, on average) to eventually obtain the same adult body size as progeny developing from eggs laid by low-density-reared females.

MATERIALS 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 geographic 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*; paloverdes; Fabaceae: Caesalpinioideae), although only one or a few hosts may be available in any single locality.

Female *S. limbatus* oviposit directly onto host seeds in fruits 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 their mother has chosen for them. In the lab, mating and egg laying begin approximately 24–48 h postemergence. Beetles require only the resources inside of a single seed to complete development and reproduce. Thus,

neither food nor water supplementation is necessary for the following lab experiments.

In previous experiments in which the number of larvae developing within a seed was manipulated (Fox et al. 1996), both egg-to-adult development time and adult-emergence weight of *S. limbatus* were developmentally plastic; at higher density beetles emerge sooner and are smaller. Body weight of emerging *S. limbatus* is also affected by seed size (larger seeds produced larger beetles than small seeds), consistent with the hypothesis that food stress due to resource competition among larvae is directly responsible for the observed effect of density on body size of *S. limbatus*.

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

Study Populations

Beetles for this experiment were collected from two localities. On July 15, 1995, beetles were collected from seeds of *Cercidium floridum* and *C. microphyllum* along Highway 62 and Old Parker Dam Road near Earp, San Bernardino County, California (Earp population). On August 20, 1995 beetles were collected from these same hosts at numerous locations in Apache Junction, Pinal County, Arizona (Apache Junction population). These two populations are more than 240 km apart, with acceptable host plants distributed throughout the intervening region.

Beetles were collected by picking mature seed pods from more than 25 plants at each site. 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. Both laboratory populations were initiated with more than 300 field collected individuals. Each population was reared in the laboratory on *Acacia greggii* (a natural host for *S. limbatus* in Arizona and California) for about three to five generations, at 30°C, L:D 15:9 prior to this study. During the experiment, beetles were reared on *A. greggii* rather than either *C. floridum* or *C. microphyllum* because, unlike on *C. floridum* or *C. microphyllum*, survivorship of *S. limbatus* on *A. greggii* is very high at any density (Fox et al. 1996). This allows the manipulation of body size (by manipulating density) without natural selection occurring during the experiment.

Experimental Methods

To test the hypothesis that variation in body size generated by resource competition persists for multiple generations after resource competition has been relaxed, I reared experimental lines at low, medium, or high density for a single generation, producing substantial variation in body size among lines. I then reared all lines at a common density until they converged on a common average body size.

To create experimental treatments, virgin males and females were collected from isolated seeds of *A. greggii* within 24 h of adult emergence. Each beetle was weighed and then paired with a single virgin beetle of the opposite sex. These beetles are subsequently referred to as the parental generation. To create treatment lines for Generation 1, pairs were

confined in a 30-mm petri dish containing one *A. greggii* seed. Dishes were checked daily for eggs until females had laid 20 or more eggs on the seed (high-density treatment, $N = 30$ pairs in each population) or 10 or more eggs on the seed (medium-density treatment, $N = 30$ pairs, Apache Junction population only). Eggs in excess of 20 (high-density) or 10 (medium-density) were scraped from each seed. Control lines were established by confining pairs in a 30-mm petri dish (as above) with 10 *A. greggii* seeds ($N = 30$ pairs in each population). These pairs were checked daily until a female had laid an egg on each of eight or more seeds. These control larvae were reared to adult at one egg/seed (excess eggs were scraped from each seed). Beetles in all lines were reared to adult at 30°C, L:D 15:9.

Emerging progeny were collected and weighed on an electronic balance within 24 h of their emergence as adults from their rearing seed. To initiate Generation 2 of the experiment, two females and two males were randomly selected from each family within the high density and control lines (only one female and one male were selected from each family in the medium-density line), and randomly paired with a nonsibling from the same line (within populations only). This subsample of beetles chosen to be parents of Generation 2 did not differ in size from the average size of all beetles emerged in their respective lines (t -tests comparing family-mean size with size of beetles chosen to be parents of Generation 2, $P > 0.05$ for each sex, line, and population). Each pair was confined in a 30-mm petri dish with 10 *A. greggii* seeds. Dishes were checked daily for eggs until females had laid eggs on six or more seeds. Egg size (egg length and width) was recorded for two haphazardly selected eggs laid by each female (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). Egg weight was estimated from egg width and length as egg weight = $-0.035 + 0.0086(\text{egg length}) + 0.0022(\text{egg width})$. Larvae were reared to adult at one egg/seed (excess eggs were scraped from each seed), 29–30°C, L:D 15:9. As above, all emerging progeny were collected and weighed within 24 h of their emergence as adults from the seed. As will be discussed below, a third generation was unnecessary in either replicate.

The two replicates of the experiment (Apache Junction and Earp populations) were executed sequentially. Thus, although population is included in all statistical analyses to control for population and/or time effects, population differences are not discussed.

RESULTS AND DISCUSSION

In both the Apache Junction and Earp populations, beetle families reared at high density (20 eggs/seed) emerged at substantially smaller adult body sizes than families reared at 10 eggs/seed, which in turn were much smaller than beetles reared at one egg/seed (Fig. 1; Table 1). Females emerging from the high-density seeds also laid smaller eggs than females reared at lower density (Table 2), as expected due to a positive relationship between maternal body size and egg size (Fox et al. 1995a; Fox and Mousseau 1996). However, although increasing female rearing density resulted in a statistically significant decrease in egg size, this decrease was

TABLE 1. Analysis of variance for the effects of experimental lines on body size of *Stator limbatus*. Generation 1 beetles were reared under high (20 eggs/seed), medium (10 eggs/seed), or low (one egg/seed) density. Generation 2 beetles were all reared under densities of one egg/seed. Treatment means are presented in Figure 1. Results are presented for female progeny only. Results for male progeny are qualitatively the same. Family, nested within population*treatment, was included in the analysis because siblings are not independent of each other. *** $P < 0.001$.

	Generation 1		Generation 2	
	df	F	df	F
Population	1	22.07***	1	1.18 ns
Treatment	2	101.74***	2	0.44 ns
Population*treatment	1	0.02 ns	1	0.92 ns
Family (pop*treat)	138	2.99***	217	0.80 ns

very small—high-density females laid eggs that were only 4.6% and 3.3 % lighter (Apache Junction and Earp populations, respectively) than low-density-reared females (Table 2). Progeny developing from these slightly smaller eggs laid by high-density-reared mothers (Table 2) eventually attained the same adult body size as progeny developing from eggs laid by low-density mothers (Fig. 1; Table 1) by developing on average 0.5–0.8 d longer (Table 3).

Thus, there was no evidence from these two populations of *S. limbatus* that the substantial body size variation generated by variable larval density within seeds in nature and in the laboratory (e.g., Fox et al. 1996) persists across generations. Instead, although females reared at high density laid smaller eggs than females reared at lower density (although only 3–5 % smaller), larvae developing from these eggs compensated for their smaller egg size by developing longer to pupate at the same body size as beetles developing from larger eggs laid by lower-density-reared mothers.

The results from this study are consistent with general observations on maternal effects in animals: we typically find large maternal effects on early progeny life history (egg size and early development) that gradually disappear and become undetectable by the time progeny mature (Mousseau and Dingle 1991; Fox 1994a; Bernardo 1996a). This reduction in the magnitude of the maternal effect as the organism develops is likely most often due to developmental plasticity in progeny. The results of my experiment indicate that *S. limbatus* larvae are developmentally plastic. In the presence of an environmental stressor, such as food shortage (resulting from intense larval competition), they can emerge sooner and at a smaller size (see also Fox et al. 1996). In the absence of an environmental stressor, larvae modify development time as necessary to attain a genetically targeted body size, such that the large environmental effect of larval density on body size does not persist into the next generation. Similar results have been reported in another seed beetle, *Callosobruchus maculatus* (Fox 1993, 1994a; Fox and Dingle 1994). For example, in *C. maculatus*, eggs laid by older mothers are smaller than eggs laid by younger mothers, but larvae compensate for this smaller egg size by developing longer to eclose at a targeted body size. Also, using a half-sib breeding design, Fox (1994a) demonstrated that although maternally induced nongenetic variation in egg size has dramatic influences on early *C. maculatus* life history, these larvae develop toward

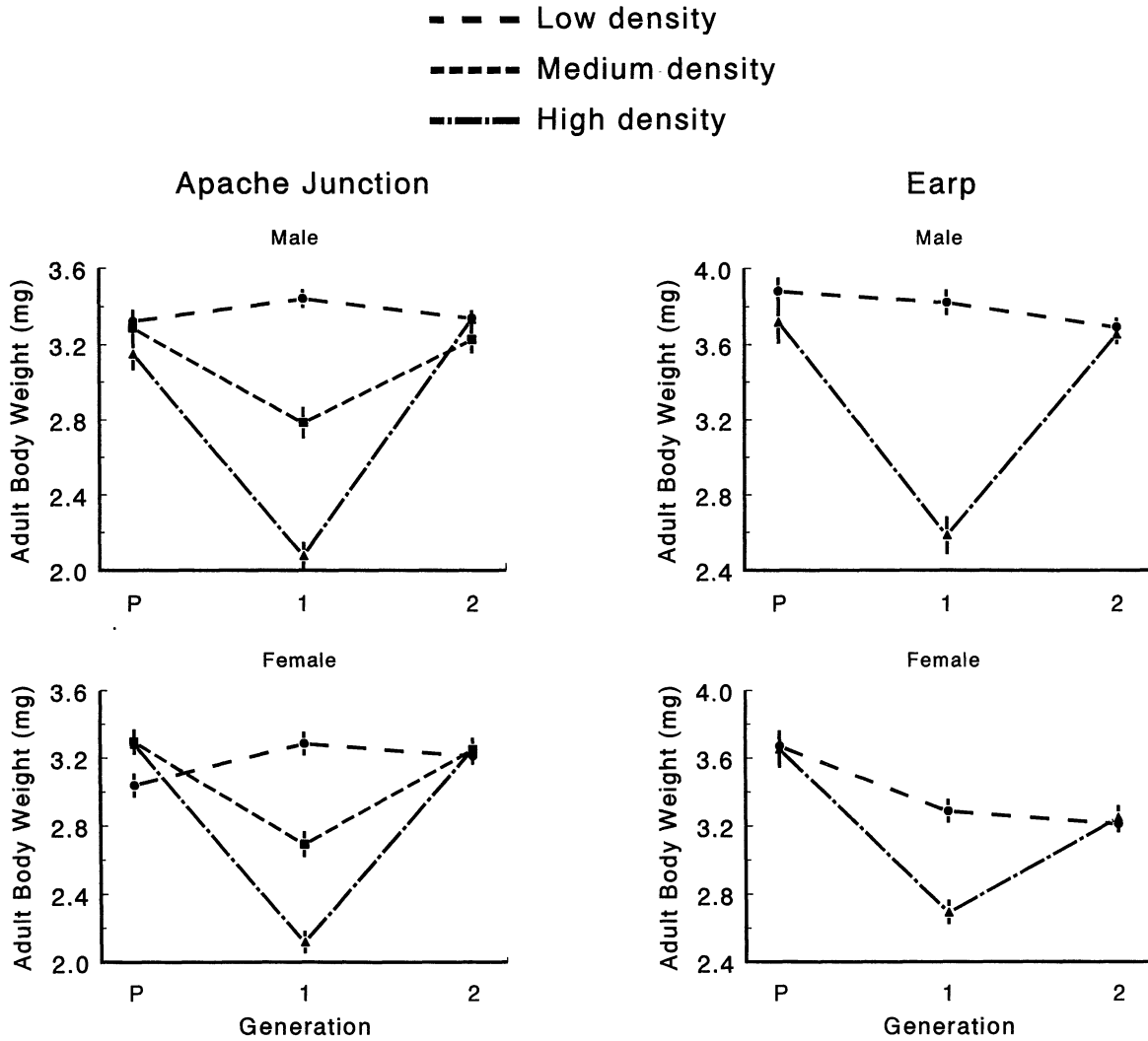


FIG. 1. Mean body size (mg) of *Stator limbatus* reared for one generation at low density (one egg/seed), then a single generation at either low (one egg/seed), medium (10 eggs/seed), or high (20 eggs/seed), and then again at low density. Note that the environmental variation in body size induced by manipulating larval density does not persist into the next generation. The slight mean decrease in body size between generations observed in all lines of the Earp population is probably due to a change in the electronic balance used to weigh the beetles (the two experiments were executed sequentially, so this change in balance did not affect the Apache Junction population). While this affected estimates of the absolute body weights, it should have had no effect on relationship between two treatments.

a genetically determined adult size, and evidence of maternal effects disappear by the time offspring reach the adult stage.

Although apparently uncommon in animals, persistence of environmental variation across multiple generations, mediated via maternal effects, has been detected in many studies with plants (Bernardo 1996a). For example, in *Plantago ma-*

jor, both maternal and grandmaternal nutrient environment affects the probability of germination, germination rate, and final spike biomass (Miao et al. 1991). Similarly, in *Plantago lanceolata*, grandparental temperature affects leaf area, leaf allometry, and the proportion of plants flowering within 94 d (Case et al. 1996). In animals, expression of maternal ef-

TABLE 2. The size of eggs (egg weight, mg/100; mean \pm SEM [number of families]) laid by female *Stator limbatus* reared under high (20 eggs/seed), medium (10 eggs/seed), or low (one egg/seed) density. Note that females reared at higher density, which are smaller, lay smaller eggs than females reared at lower density. * $P = <0.05$, ** $P = <0.001$.

	Mean egg weight (mg)		Analysis of variance		
	Apache Junction	Earp	Source	df	F
Low density	1.95 \pm 0.03 (57)	2.11 \pm 0.03 (50)	Population	1	43.48**
Medium density	1.92 \pm 0.03 (29)		Treatment	2	3.77*
High density	1.86 \pm 0.02 (52)	2.04 \pm 0.03 (50)	Pop*treat	1	0.23 ns

TABLE 3. Development time in days (mean \pm SEM [number of families]) of *Stator limbatus* females developing from eggs laid by mothers reared at high (20 eggs/seed), middle (10 eggs/seed), or low (one egg/seed) density. Data are for female progeny. Patterns for male progeny are qualitatively identical. Note that progeny developing from eggs laid by high density females took, on average, 0.5–0.8 d longer to reach their final adult body size than progeny developing from eggs laid by low density females. ** $P < 0.01$, *** $P < 0.001$.

	Mean development time (d)		Analysis of variance		
	Apache Junction	Earp	Source	df	F
Low density	23.3 \pm 0.1 (53)	23.7 \pm 0.2 (45)	Population	1	12.26***
Medium density	23.7 \pm 0.3 (28)		Treatment	2	6.54**
High density	23.8 \pm 0.1 (49)	24.5 \pm 0.2 (48)	Pop*treat	1	0.68 ns
			Family (pop*treat)	218	1.80***

fects variation by adult progeny appears to be more rare, but not unknown. For example, in many aphids, such as *Myzus persicae* and *Megoura viciae*, grandparental photoperiod affects the production of alate (and sexual) progeny (Lees 1959; Blackman 1975) with more alates produced at shorter photoperiods. Likewise, diapause in aphids can be triggered by the environmental conditions experienced by grandparents (in which photoperiod stimulates the production of sexual morphs, which mate and lay diapausing eggs; Blackman 1975).

Despite previous observations that some seed beetles are developmentally plastic and that environmental effects rarely, if ever, persist into a third generation in animals, I expected the large environmental effects on body size observed in *S. limbatus* to persist across generations in this experiment. Previous experiments have examined the persistence across generations of environmental variation in body size, but generally only in unstressed populations of animals showing substantially less variation in body size than *S. limbatus* (e.g., Fox 1994a). In *S. limbatus*, food stress in the form of high larval density (e.g., 20 eggs/seed in this paper) causes larvae to emerge on average 34% and 26% smaller (Apache Junction and Earp populations, respectively) than progeny reared at low density, and produces variation in body size of over an order of magnitude (largest low-density beetles relative to smallest high-density beetles). If these high-density-reared females had laid eggs that were likewise 25–35% smaller, larvae would have needed to develop substantially longer to make up for this disadvantage. However, high-density females did not lay eggs that were 25–35% smaller. Instead, these high-density females laid eggs that were only about 5–3% smaller by weight (Apache Junction and Earp populations, respectively), compensating for their small body size by increasing egg size. Subsequently, their progeny developed slightly longer to emerge at the same body size as normal, nonstressed beetles.

That egg size does not decrease proportionally with female body size may represent a life-history adaptation to intense selection on egg size of *S. limbatus* in nature (Fox and Mousseau 1996; Fox et al. 1997). When larvae are reared on the blue paloverde, *Cercidium floridum*, there appears to be a threshold egg size below which larval mortality is nearly 100%. Although this threshold effect of egg size on larval survivorship does not exist for larvae reared on *A. greggii*, both populations examined in this study use *C. floridum* in nature in addition to *A. greggii* (in fact, *C. floridum* is more common than *A. greggii* for both populations). Thus, selec-

tion should favor females that lay eggs larger than the threshold size for penetrating the coat of a *C. floridum* seed, regardless of their body size. Because larval competition is common in natural populations of *S. limbatus* (Mitchell 1977; Siemens and Johnson 1992), resulting in small females, we may expect selection to favor a decoupling of body size variation from egg size under conditions of food stress.

In addition to a partial decoupling of egg-size and body-size variation, *S. limbatus* larvae are developmentally plastic in response to variable food stress. This also may be an adaptation to variable larval densities in nature. In many insects, increasing larval density substantially reduces the survivorship of larvae (Wilson 1994 and references cited therein). However, in *S. limbatus*, increasing larval density results in earlier emergence at a smaller size, and only a small decrease in egg-to-adult survivorship. Among-population comparisons in another seed beetle, *C. maculatus*, demonstrate that life-history responses to larval competition can respond to selection. In some highly competitive *C. maculatus* populations, larval survivorship decreases substantially with increasing larval density, while in less competitive populations larvae respond to increasing larval competition by pupating at smaller sizes, with little effect on egg-to-adult survivorship (Messina 1991). Similar among-population differences are suggested for *S. limbatus*: Siemens and Johnson (1992) reported large effects of larval density of larval survivorship, although in a separate study on a different population of beetles Fox et al. (1996) found at most a weak effect of larval density on larval survivorship.

In summary, body size in *S. limbatus* varies by as much as an order of magnitude, due largely to variation in the intensity of larval competition within host seeds. Also, mortality of *S. limbatus* on *A. greggii* is very low, even at high larval density, such that selection on body size can be largely eliminated during experiments (Fox et al. 1996). Thus, this animal provided an excellent opportunity to demonstrate the persistence of environmental variation in body size across generations. However, I found that environmentally induced body size variation does not persist across generations in *S. limbatus*. Instead, developmental plasticity allows progeny to compensate for reduced egg size associated with higher maternal density. This failure to find persistence of body size variation across generations in this ideal study system is consistent with observations from other animal studies, and suggests that crossgenerational persistence of maternal effects is likely to be very rare in animals.

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LITERATURE CITED

- BERNARDO, J. 1996a. Maternal effects in animal ecology. *Am. Zool.* 36:83–105.
- . 1996b. The particular maternal effect of propagule size, especially egg size: patterns, models, quality of evidence and interpretations. *Am. Zool.* 36:216–236.
- BLACKMAN, R. L. 1975. Photoperiodic determination of the male and female sexual morphs of *Myzus persicae*. *J. Insect Physiol.* 21:435–453.
- CASE, A. L., E. P. LACEY, AND R. G. HOPKINS. 1996. Parental effects in *Plantago lanceolata* L. II. Manipulation of grandparental temperature and parental flowering time. *Heredity* 76:287–295.
- FALCONER, D. S. 1965. Maternal effects and selection response. *Genetics Today* 3:763–774.
- FLEMING, I. A., AND M. R. 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* 96:139–146.
- . 1994a. Maternal and genetic influences on egg size and larval performance in a seed beetle: multigenerational transmission of a maternal effect? *Heredity* 73:509–517.
- . 1994b. The influence of egg size on offspring performance in the seed beetle, *Callosobruchus maculatus*. *Oikos* 71:321–325.
- FOX, C. W., AND H. DINGLE. 1994. Dietary mediation of maternal age effects on offspring performance in a seed beetle (Coleoptera: Bruchidae). *Funct. Ecol.* 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* 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* 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. *Anim. Behav.* 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, C. W., J. D. MARTIN, M. S. THAKAR, AND T. A. MOUSSEAU. 1996. Clutch size manipulations in two seed beetles, *Stator limbatus* and *S. beali*: consequences for progeny fitness. *Oecologia* 108:88–94.
- FOX, C. W., M. S. THAKAR, AND T. A. MOUSSEAU. 1997. Egg size plasticity in a seed beetle: an adaptive maternal effect. *Am. Nat.* 149:149–163.
- JOHNSON, C. D., AND J. M. KINGSOLVER. 1976. Systematics of *Stator* of North and Central America (Coleoptera: Bruchidae). US Dep. Agric. Tech. Bull. 1537:1–101.
- JOHNSON, C. D., J. M. KINGSOLVER, AND A. TERAN. 1989. Sistemática del género *Stator* (Insecta: Coleoptera: Bruchidae) en Sudamérica. *Opera Lilloana* 37:1–105.
- KAPLAN, R. H. 1991. Developmental plasticity and maternal effects in amphibian life histories. Pp. 794–799 in E. C. Dudley, ed. *The unity of evolutionary biology*. Vol. 2. Dioscorides Press, Portland, OR.
- LEES, A. D. 1959. The role of photoperiod and temperature in the determination of parthenogenetic and sexual forms in the aphid *Megoura viciae* Bucton. I. The influence of these factors on apterous virginoparae and their progeny. *J. Insect Physiol.* 3:92–117.
- MESSINA, F. J. 1991. Life-history variation in a seed beetle: adult egg-laying vs. larval competitive ability. *Oecologia* 85:447–455.
- MIAO, S. L., F. A. BAZZAZ, AND R. B. PRIMACK. 1991. Persistence of maternal effects in *Plantago major*: the third generation. *Ecology* 72:1634–1642.
- MITCHELL, R. 1977. Bruchid beetles and seed packaging by palo verde. *Ecology* 58:644–651.
- MOUSSEAU, T. A., AND H. DINGLE. 1991. Maternal effects in insect life histories. *Annu. Rev. Entomol.* 36:511–534.
- MOUSSEAU, T. A., AND C. W. FOX, EDs. In press. *Maternal effects as adaptations*. Oxford Univ. Press, Oxford.
- NILSSON, J. A., AND C. D. JOHNSON. 1993. Laboratory hybridization of *Stator beali* and *S. limbatus*, with new host records for *S. limbatus* and *Mimosstes amicus* (Coleoptera: Bruchidae). *Southwest. Nat.* 38:385–387.
- REZNICK, D. N. 1991. Maternal effects in fish life histories. Pp. 780–793 in E. C. Dudley, ed. *The unity of evolutionary biology*. Vol. 2. Dioscorides Press, Portland, OR.
- RISKA, B. 1991. Introduction to the symposium. Pp. 719–724 in E. C. Dudley, ed. *The unity of evolutionary biology*. Vol. 2. Dioscorides Press, Portland, OR.
- RISKA, B., J. J. RUTLEDGE, AND W. R. ATCHLEY. 1985. Covariance between direct and maternal genetic effects in mice, with a model of persistent environmental influences. *Genet. Res.* 45:287–297.
- ROACH, D. A., AND R. D. WULFF. 1987. Maternal effects in plants. *Annu. Rev. Ecol. Syst.* 18:209–235.
- 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* 82:408–423.
- . 1992. Density-dependent egg parasitism as a determinant of clutch size in bruchid beetles (Coleoptera: Bruchidae). *Environ. Entomol.* 21:610–619.
- 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.
- WILSON, K. 1994. Evolution of clutch size in insects. II. A test of static optimality models using the beetle *Callosobruchus maculatus* (Coleoptera: Bruchidae). *J. Evol. Biol.* 7:365–386.

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