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ONTOGENY OF SUBTLE SKELETAL ASYMMETRIES IN INDIVIDUAL LARVAE OF THE SAND DOLLAR *DENDRASTER EXCENTRICUS*

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Fluctuating asymmetry (FA), defined as the distribution of small random deviations from bilateral symmetry in a sample of organisms, has received considerable attention in recent evolutionary and behavioral literature (Markow 1994). The degree of asymmetry exhibited by a single organism presumably results from small independent disruptions of normal development caused by random differences of internal and external environment on each side. FA is used in evolutionary studies as a measure of genetic quality, developmental robustness, and environmental tolerance. FA may reflect genetic quality because individual asymmetry is often inversely correlated with heterozygosity (Mulvey et al. 1994), and hybrids are often more asymmetrical than either of their parent species (Graham 1992). Behavioral studies of the "good genes" model of mate choice commonly assume individual asymmetry is inversely correlated with genetic quality. These studies have also extended the association between genotypic and phenotypic quality, and asymmetry by showing that females often prefer symmetrical males and that symmetrical males, may be more successful foragers (Møller 1992, 1994; and reviewed in Møller and Pomiankowski 1994). Asymmetry is also associated with environmental stress such as pollution and thermal stress (Graham et al. 1993). Paleontological studies have attempted to apply these results to fossil groups. Smith (1994) measured FA in trilobite species throughout the Cambrian and early Ordovician, in an attempt to determine if developmental robustness increased after the Cambrian explosion. Finally, Palmer et al. (1994) have looked to random asymmetries for clues to the origin of large genetically determined asymmetries like those seen in fiddler-crab claws and gastropod torsion.

Although FA and other patterns of asymmetry are assumed to result from developmental processes, few studies have directly addressed changes in asymmetry during ontogeny (but see Chippindale and Palmer 1993; and for an indirect approach see Hallgrimson 1993). Such studies are of interest because associations between deviations from symmetry among traits and within traits through time may yield insights into both the causes of asymmetries and mechanisms controlling the development of bilaterally symmetrical characters.

The way asymmetries vary during ontogeny can be used to determine the relative contributions of intrinsic and extrinsic factors to asymmetries, and thus suggest which factors are most clearly reflected by both an individual's asymmetry and the population distribution of asymmetries. Here I consider four factors that might influence deviations from symmetry, and their correlations through ontogeny and among traits (Table 1). These factors might act singly or in concert during development. First, asymmetry may reflect individual quality. For example, individuals of low genetic quality may be less able to develop normally in the face of small perturbations during development (Watson and Thornhill 1993). Low quality individuals may also be less effective at foraging or selecting appropriate environments, which could cause them to experience higher levels of physiological stress than higher quality individuals. If asymmetry is a strong reflection of individual quality, then asymmetries should be correlated among traits and within a trait through time.

Second, asymmetry can represent the persistence of previous asymmetries or the inability of the individual to detect or compensate for asymmetries. For example, changes in asymmetry of structures that cannot grow between molts, like bird feathers and arthropod appendages, may be extremely limited (Chippindale and Palmer 1993). Strong constraints on compensation for asymmetries should produce a correlation of asymmetry within a character through time, since reductions in existing asymmetry are limited, but not necessarily between characters. In addition, if compensation for asymmetry is constrained the sign R − L (right minus left) is unlikely to change. If this is the case, the correlation of actual asymmetries (R − L) through time should be equal to or greater than the correlation of the amount of asymmetry (|R − L|). If reduction and compensation for asymmetries is not constrained, the correlations between actual asymmetries through time may be less than the correlations between the amount of asymmetry.

The third factor that could influence asymmetries is the proximity to extrinsic stresses. Environmental factors like exposure to pesticides, extreme temperatures, and parasites have been shown to increase asymmetries (Parsons 1990). Asymmetries that are strongly correlated among characters, but not through time, may reflect temporal proximity to stresses that affected the whole organism.

Finally, dynamic interactions between complex developmental feedback systems, extrinsic perturbations, and developmental thresholds may lead to no clear patterns of correlations among asymmetries. Absence of such correlations my reflect nonlinear dynamic developmental processes and feedback loops like those described by Graham et al. (1994) or

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TABLE 1. Possible factors influencing the ontogenies of asymmetries and the correlations they would create.

Factor	Correlation through time	Correlation among characters	Comments
Individual quality	yes	yes	Correlation through time: $\|R - L\| > R - L$ Correlation among characters: $\|R - L\| > R - L$
Constraint on compensation	yes	no	Correlation through time: $R - L > \|R - L\|$
Temporal proximity to specific stress	no	yes	
Dynamic morphogenesis	maybe	maybe	Correlations depend on the model

stochastic variation. Clearly several of these factors could operate in any system and the relative contribution of each factor could change with environmental conditions. To explore how the correlations among asymmetries change during development, I followed the early skeletal development of individual sand dollar (*Dendraster excentricus*) larvae.

MATERIALS AND METHODS

Adult *D. excentricus* were collected intertidally from False Bay, San Juan Island, and Ship Bay in East Sound, Orcas Island, Washington, in the spring of 1994. Animals were spawned between July 18 and September 18, 1994, using intracoelomic injection of 0.5 M KCl or electrical stimulation (Strathmann 1987). Several males and females were used to produce each of the eight cohorts. Initially embryos were kept in a monolayer culture in custard dishes at room temperature (19–22°C) in 0.45 μm filtered sea water. The unicellular alga *Rhodomonas* sp. was provided ad libitum after larvae had reached the prism stage and were able to feed. On day 2 (approximately 48 h after fertilization) individual four-armed larvae were selected haphazardly from the culture and measured. The larva was placed flat on a slide with the anterior-posterior axis parallel to the plane of the slide and the ventral side down. Each larva was carefully trapped under the coverslip to prevent it from moving and to orient it so that the skeletal rods were as parallel to the focal plane as possible. The lengths of right and left anterolateral, postoral, and posterodorsal skeletal rods were measured (Fig. 1) with an ocular micrometer on a compound microscope with a total magnification of 200X. Posterodorsal skeletal rods were not measure on day 2 because they had not yet begun to develop. Larvae were subsequently kept individually in 4-mL well plates in 0.45 μm filtered sea water at room temperature (20–22°C) with initial *Rhodomonas* concentrations of 100,000 cells mL^{-1}. On days 4, 6, and 8 after fertilization, each larva was remeasured and moved to a new well plate with new food and water.

In an attempt to control for the effects of handling stress, some larvae were only measured on day 2 and day 8. The asymmetries in these larvae did not differ from the larvae that were measured on all four days, and they were excluded from this analysis because the temporal correlations could not be calculated for them. In addition, any animal that was not measured on all four days was excluded from the analysis. Unequal sample sizes are caused by a few instances where one set of arms could not be measured on a single day. During August sibling larvae from the same initial cultures were maintained in a group culture at the same density and fed the same algal concentrations as the larvae that were reared individually. The average arm lengths for these larvae were compared to the arm lengths of the animals used in this study to determine if these conditions were adequate for normal growth. Because the rate of arm growth is highly temperature dependent and varies in response to food concentrations (Strathmann et al. 1992) it is difficult to make detailed comparisons of arm length in different studies.

TABLE 2. Summary of lengths and asymmetries of *Dendraster excentricus* larval arms.†

	Individually reared larvae						Group culture	
	R − L			(R + L)/2	|R − L|		Length	
	Mean (SD)	Skew	Kurtosis	Mean (SD)	Mean (SD)	*n*	Mean (SD)	*n*
Anterolateral								
Day 2	0.30 (34.0)	2.45*	17.73*	148.9 (52.3)	16.8 (29.6)	151	142.1 (19.7)	100
Day 4	2.20 (64.2)	0.94*	10.92*	305.6 (51.5)	32.8 (55.2)	150	283.8 (38.9)	200
Day 6	5.53 (73.5)	3.48*	18.88*	397.9 (71.1)	35.1 (64.7)	150	370.6 (65.5)	200
Day 8	3.95 (84.8)	2.47*	12.36*	470.7 (97.2)	49.2 (69.1)	146	540.9 (85.9)	154
Postoral								
Day 2	3.73 (37.1)	2.72*	22.43*	190.2 (52.2)	17.4 (33.0)	151	190.9 (22.4)	100
Day 4	8.29 (50.0)	−0.02	6.28*	336.0 (57.4)	34.6 (37.0)	150	292.5 (45.6)	200
Day 6	−9.40 (102.7)	−1.40*	7.91*	395.2 (73.2)	54.6 (87.3)	150	335.0 (66.9)	200
Day 8	−57.01* (110.9)	−1.68*	2.31*	440.8 (88.5)	74.7 (99.8)	150	394.8 (55.9)	198
Posterodorsal								
Day 4	19.67* (34.6)	−0.11	1.97*	107.5 (51.0)	30.5 (25.4)	141	39.9 (24.9)	200
Day 6	16.32* (59.7)	−1.30*	5.05*	264.2 (85.8)	42.8 (44.6)	149	153.8 (68.7)	200
Day 8	27.53* (76.0)	1.79*	6.98*	380.3 (101.1)	50.5 (63.0)	149	254.4 (58.5)	200

† All measurements are in μm.
* Significant at $\alpha < 0.05$ with a separate Bonferroni correction for each column.

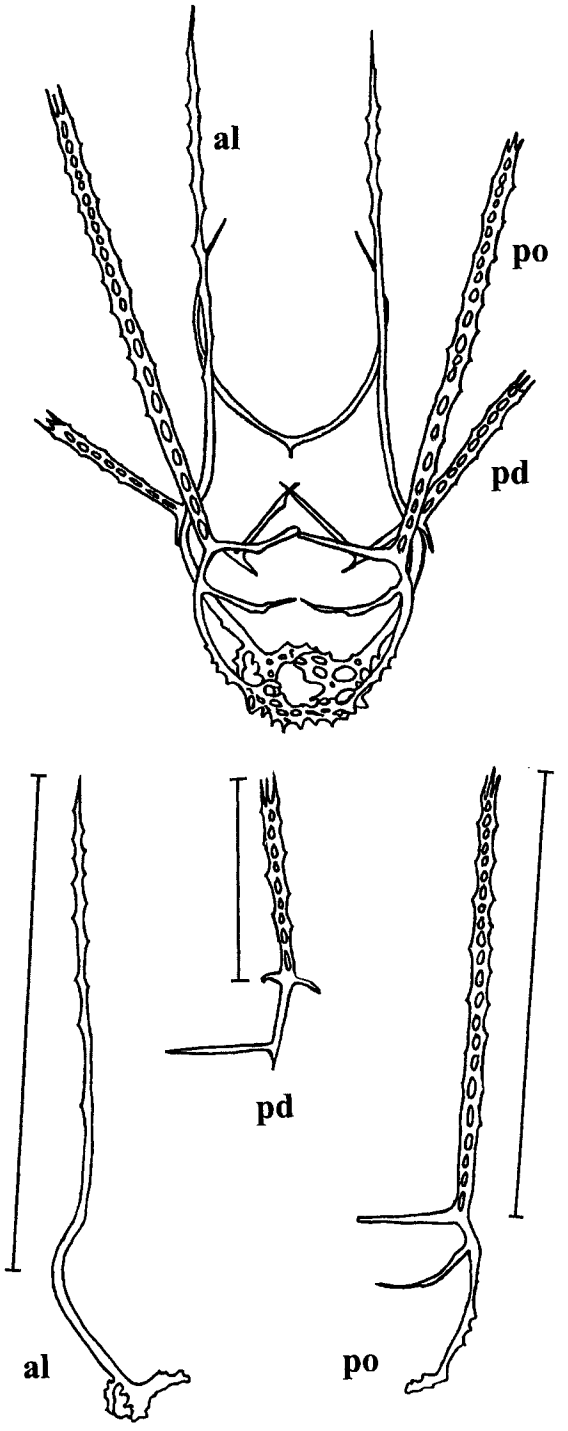

FIG. 1. (Top) Larval skeleton of a typical Clypeasteroid; al = anterolateral rods; pd = posterodorsal rods; po = postoral rods. (Bottom) Larval arm rods showing the landmarks used to measure their length.

Measurement error was estimated following Palmer (1994). Because extensive handling can damage larvae, repeated measurements could not be made for each larva on each day in the study. Five larvae of each age were selected haphazardly and measured independently (but not blindly) five times. Each larva was positioned on the slide, measured, removed from the slide, and replaced in the well plate. This procedure was repeated five times by the end of which some larvae were clearly damaged. Analyses of variance (ANOVAs) were conducted to test for the relative effects of measurement error compared to between-sides variance.

TABLE 3. Estimates of measurement error (μm) based on repeated measurements of five individual larvae.

	Mean squares from ANOVA			
	Individual	Side	Individual × side†	Error
Anterolateral				
Day 2	9567	24.2	1354	19.7
Day 4	9234	3894	6497	7.0
Day 6	48,214	4.0	24,059	13
Day 8	4699	648	7293	65
Postoral				
Day 2	3779	2140	1659	12.0
Day 4	12,804	56	351	4.7
Day 6	13,682	589	6272	7.1
Day 8	74,902	1811	421	25
Posterodorsal				
Day 4	9924	1925	1034	7.0
Day 6	20,741	4143	3430	43
Day 8	48,988	6877	882	55
df	4	1	4	34

† Individual × side effect was significant for all measurements ($P < 0.0005$).

I used the difference between the lengths of the right and left arms (R − L) as a measure of asymmetry. This measure was not dependent on body size as measured by a regression of R − L on R + L for the character on all days combined (anterolateral: $r = 0.004$, $P > 0.9$, postoral: $r = 0.001$, $P > 0.9$, posterodorsal: $r = 0.023$, $P > 0.7$, $n = 600$). All measurements are given in microns.

I used *t*-tests to determine whether R − L deviated from the ideal distribution of FA (normal distribution with a mean of zero) for each skeletal arm on each day (using standard errors and procedures given in Sokal and Rohlf 1981). Pearson correlation coefficients were calculated for R − L and |R − L| among characters and within characters over time using SYSTAT version 5.1. Tablewide Bonferroni probabilities were calculated according to Rice (1989). The effect of individual and age on changes in asymmetry were tested using a repeated-measures ANOVA, with amount of asymmetry on all four days as the dependent variables and animals as the independent variable. The repeated measures ANOVA on |R − L| is a form of Levene's test for differences in variability among days.

RESULTS

The distribution of asymmetry in larval skeletal rods did not generally fit the ideal distribution of FA (Table 2). Both the anterolateral and postoral rods showed few departures from a mean of zero, while the posterodorsal rods showed a significant right-bias directional asymmetry. Skew and kurtosis were significant for all characters, and the variance increased as the larvae grew. Arm lengths for the individually reared larvae where similar to those that were reared in group

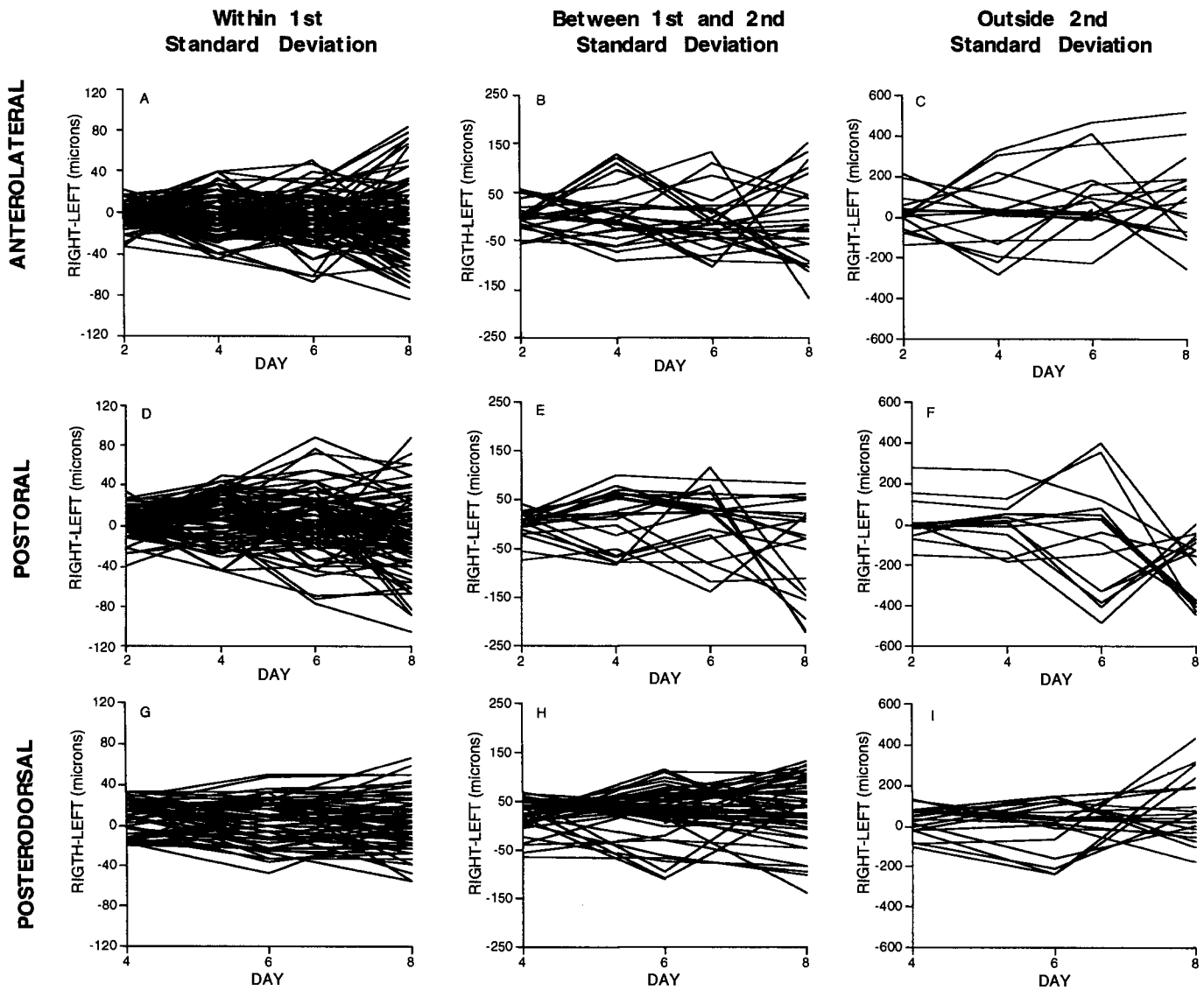

FIG. 2. Changes in actual skeletal asymmetries (R − L) though time for the anterolateral (A, B, C), postoral (D, E, F), and posterodorsal (G, H, I) arms. Those animals that were never more than one standard deviation from the mean (A, D, G); those that were more than one standard deviation from the mean on at least one day, but never more than two standard deviations from the mean (B, E, H); and those that were more than two standard deviations from the mean on at least one day (C, F, I) are plotted separately. Ninty-five percent confidence intervals for measurement error were calculated as $2\sqrt{MS_{err}}$ for anterolateral (day 2 = 8.8 μm; day 4 = 5.3 μm; day 6 = 7.2 μm; day 8 = 16.1 μm), postoral (day 2 = 6.9 μm; day 4 = 4.3 μm; day 6 = 5.3 μm; day 8 = 10.0 μm), and posterodorsal (day 4 = 5.3 μm; day 6 = 13.1 μm; day 8 = 11.7 μm).

cultures (Table 2) and measurement error was smaller than the between-sides variance (Table 3).

Both the magnitude and direction of changes in asymmetry varied during development (Fig. 2); significant correlations were observed between asymmetries both among characters on a given day and within a character through time (Tables 4, 5, 6, and 7). In some cases the correlations between actual asymmetries (R − L) were stronger than between amount of

TABLE 4. Pearson correlation coefficients among actual asymmetries (R − L) on a given day. Tablewide Bonferroni probabilities: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.005$.

	Day 2	Day 4	Day 6	Day 8
Postoral vs. anterolateral	0.375***	0.475***	0.310***	−0.013
Postoral vs. posterodorsal	—	0.311***	0.029	−0.201
Anterolateral vs. posterodorsal	—	0.339***	0.296***	0.253*
n	141	141	149	146

TABLE 5. Pearson correlation coefficients among amounts of asymmetry of each character (|R − L|) on a given day. Tablewide Bonferroni probabilities: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.005$.

	Day 2	Day 4	Day 6	Day 8
Postoral vs. anterolateral	0.325***	0.304***	0.304***	0.232*
Postoral vs. posterodorsal	—	0.130	0.415***	0.242*
Anterolateral vs. posterodorsal	—	0.356***	0.299***	0.190
n	141	141	149	146

asymmetry |R − L|, sometimes correlations between the amounts of asymmetry were stronger than between the actual asymmetries and sometimes the correlations were comparable. In several cases, especially in the anterolateral arms, the correlations of the amount of asymmetry through time were considerably higher than the correlations between different arms on the same day. Analysis using Spearman rank correlations did not qualitatively alter the results reported here.

The results of the repeated-measures ANOVA (Table 8) also support the fact that there is no consistent relationship between asymmetries through time. Asymmetries (both [R − L] and |R − L|) were significantly affected by day, individual and day × individual interaction for all characters except the anterolaterals. The day effect for |R − L| indicates a difference in variability among days. Although the assumption of normality is not met for actual asymmetry (R − L), the results of ANOVAs are relatively robust to violation of this assumption, and both the univariate and multivariate statistics were in agreement. These three relationships show that individual asymmetry changes with time, but the way it changes differs among larvae.

DISCUSSION

The complicated pattern of correlations of asymmetries between days and among characters suggests that changes in larval skeletal asymmetries are the result of dynamic morphogenesis. Each of the first three factors that contribute to asymmetry (Table 1) receive support from the correlations among some characters across some days, but none of them are clearly the most important. Plots of individual trajectories of asymmetries (Fig. 2) show that asymmetries can change drastically over the course of two days. This indicates that there is probably not a biological constraint on reduction and compensation for these asymmetries. The strong correlations found for some characters between days and among some characters within a day suggest that some of the variation in asymmetry may reflect individual quality. The presence of correlations through time that are often on the order of magnitude of the correlations among characters suggests that the effects of proximity to a temporally constrained stress are small relative to other factors. As the time between measurements increases, the correlations also decrease, further supporting the idea that there is no long-term constraint on compensation. Finally, the low correlations obtained for some characters and the lack of a consistent pattern of correlations for both R − L and |R − L| suggests that some of the changes in asymmetry of *D. excentricus* larvae represent dynamic morphogenesis or stochastic processes. The dynamic morphogenesis model is supported by the clumping of some of the asymmetry trajectories (Fig. 2; especially the extremely asymmetrical postoral arms), which is suggestive of some type of stable trajectory or "attractor" as discussed by Graham et al. (1994). If stochastic processes were solely responsible for asymmetries, the asymmetries measured in this study should have been normally distributed.

The asymmetries in this study did not meet the strict definition of FA because they were not distributed normally with a mean of zero. Palmer (1994) Palmer and Strobeck (1992) assert that distributions of asymmetries within a population that do not meet these criteria may represent the effects of factors other than developmental noise and developmental stability, such as genetic predisposition (e.g., handedness) or

TABLE 6. Pearson correlation coefficients for actual asymmetries (R − L) of each arm through time. Tablewide Bonferroni probabilities: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.005$.

	Day 2	Day 4	Day 6	Day 8
Anterolateral				
Day 2	1			
Day 4	0.324***	1		
Day 6	0.206	0.641***	1	
Day 8	−0.273	0.250	0.420***	1
Postoral				
Day 2	1			
Day 4	0.637***	1		
Day 6	0.385***	0.414***	1	
Day 8	−0.063	−0.018	−0.116	1
Posterodorsal				
Day 4	—	1		
Day 6	—	0.481***	1	
Day 8	—	−0.118	−0.021	1

TABLE 7. Pearson correlation coefficients for amount of asymmetry (|R − L|) of each arm through time. Tablewide Bonferroni probabilities: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.005$.

	Day 2	Day 4	Day 6	Day 8
Anterolateral				
Day 2	1			
Day 4	0.220	1		
Day 6	0.118	0.816***	1	
Day 8	0.206	0.768***	0.702***	1
Postoral				
Day 2	1			
Day 4	0.679***	1		
Day 6	0.293*	0.292*	1	
Day 8	0.313**	0.221	0.197	1
Posterodorsal				
Day 4	—	1		
Day 6	—	0.491*	1	
Day 8	—	0.263*	0.491***	1

TABLE 8. Univariate statistics for the repeated-measures analysis of variance testing for the effect of individual and day on actual asymmetry (R − L) and amount of asymmetry (|R − L|) (μm).

		R − L		|R − L|	
	df	MS	*P*	MS	*P*
Anterolateral					
Between subjects					
Individual	1	102	0.9	33,557	0.035
Error	144	7891		7419	
Within subjects					
Day	3	7862	0.059	15,097	< 0.001
Day × individual	3	9102	0.035	3469	
Error	432	3151		1642	
Postoral					
Between subjects					
Individual	1	248,036	< 0.001	500,894	< 0.001
Error	148	6591		4485	
Within subjects					
Day	3	295,760	< 0.001	184,700	< 0.001
Day × individual	3	174,610	< 0.001	107,682	< 0.001
Error	444	5039		3378	
Posterolateral					
Between subjects					
Individual	1	15,038	0.05	64,228	< 0.001
Error	138	3835		3277	
Within subjects					
Day	2	30,473	< 0.001	27,682	< 0.001
Day × individual	2	29,946	< 0.001	16,456	< 0.001
Error	276	3216		1422	

ontogenetic interactions between sides. However, other factors could create normally distributed asymmetries, and asymmetries produced solely by developmental noise and developmental stability could be non-normally distributed (Graham et al. 1994). In fact, reaction-diffusion models of morphogenesis can create both normal and bimodal distributions of asymmetries (Graham et al. 1994). In cases where initial asymmetry is correlated with changes in asymmetry, the tails of the asymmetry distribution are expected to be elongated or foreshortened. Such changes in the shape of distributions of asymmetry could also be due to other factors such as differential survival. Since we do not know how asymmetries change through time for most systems used in FA studies, it is premature to assume that the shape of the asymmetry distribution at one point in time reflects the shape of asymmetries at previous or subsequent times or stages in development.

Most previous studies of fluctuating asymmetry have treated asymmetries as constant morphological characters. This leads to the assumption that the distribution of asymmetries observed at one point in time (often lumped for many animals at different developmental stages or ages) represents some end-point value reflecting mostly intrinsic or extrinsic factors. Further studies are necessary to understand the dynamic interactions that produce the distribution of asymmetries observed at any one time in development and to determine whether changes in the shape of asymmetry distributions can be used to predict which factors have the most influence on changes in asymmetry.

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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,