low power SEMs (Figures 2, 8, and 12) is 100 µm (shown in Figure 20, while for high magnification SEMs (Figures 4, 5, 9, 10, 13, and 14) is 1 µm (shown in Figure 4).

Our light micrographs verify the well-known fact that *lz* (red-eyed lz^{77a7} [Figures 6 and 7] and white-eyed lz^{r15} [Figure 11]) compound eyes are shiny compared with those of our red-eyed (Figure 1) and white-eyed (Figure 3) controls. At the resolution of the dissection microscope, it is not possible to state whether *lz* ocelli look different from the corresponding wild-type controls (white-eyed control Figure 3 arrow, red-eyed lz^{77a7} Figure 7 arrow, white-eyed lz^{r15} Figure 11 arrow). Our low power SEM's verify for the gross abnormalities of the compound eyes and present (to our knowledge for the first time) a reasonably normal ocellar countenance (compare Figure 8 red-eyed lz^{77a7} and Figure 12 white-eyed lz^{r15} with Figure 2 wild-type).

High power SEMs show that red-eyed lz^{77a7} (Figure 9) and white-eyed lz^{r15} (Figure 13) compound eyes do have corneal nipples which look much like those of control flies (Figure 4) except with more irregularities. For ocelli, red-eyed lz^{77a7} (Figure 10) and white-eyed lz^{r15} (Figure 14) exhibit a fairly normal corneal nipple array compared with that of control flies (Figure 5).

Based on the importance of corneal nipples as an antireflection coating and the shininess of the *lz* eyes, we might have expected to see a greater disturbance in the corneal nipple array of *lz* compound eyes. The subtlety of the nipple disarray suggests alternative explanations for the glossy compound eyes. Probably the irregularity of the array and curvature of the cornea over each facet is the primary determinant of shiny compound eyes. At the level of surface morphology, we conclude that *lz* ocelli are largely normal.

Acknowledgments: Gail Flores of Utpal Banerjee's laboratory at UCLA provided the *lz* mutants. Heidi Barnhill helped with SEM, Jon Wagnon helped in the darkroom, and Jeremy Beatty helped with light microscopy.

References: Batterham, P., *et al.*, 1996, J. Neurogenet. 10:193-220; Bernhard, C.G., *et al.*, 1970, Z. vergl. Physiologie 67:1-25; Bernhard, C.G., *et al.*, 1965, Acta. Physiol. Scand. 63(supp. 243):1-79; Crew, J.R., *et al.*, 1997, Daga, A., *et al.*, 1996, Genes and Develop. 10:1194-1205; Flores, G.V., *et al.*, 1998, Development 125:3681-7; Stark, W.S., *et al.*, 1989, J. Neurogenet. 5:127-153.

Ovarian fluctuating asymmetry: a stable property among *Drosophila* species.

Moreteau, B., A. Brochen, E. Pla, and J. R. David. Laboratoire Populations, Génétique et Evolution, C.N.R.S., 91198 Gif sur Yvette Cedex, France.

Fluctuating asymmetry (FA), which estimates the imprecision with which bilateral traits are determined during the development, is receiving increasing attention among evolutionary biologists (Palmer and Strobeck, 1986; Moeller and Swaddle, 1997).

FA is a special kind of phenotypic plasticity and is known to increase under environmental stress. A major, hotly debated problem is to know whether FA *per se* may be a target of natural selection (Moeller and Thornhill, 1997). Such a possibility should imply some genetic determinism of this trait.

FA is difficult to estimate for metrical traits (*e.g.*, fruit fly wing length) because of possible measurement errors (see Moeller and Swaddle). By contrast, ovaries are made of numerous tubules

Table 1. Basic data concerning ovariole number and fluctuating asymmetry in 18 species of the *D. obscura* group. Species were grown at 21°C, and for each of them, 25 females were analyzed. *D. narragansett* in this table was misidentified and corresponds in reality to another strain of *D. imaii*. This does not however invalidate our conclusions on FA.

	Ovariole no.			Fluctuating asymmetry			
				FA-abs		FA-rel	
Species	m	s.d.	CV	m	s.d.	m	s.d.
affinis	32.12	2.32	7.21	1.88	1.36	11.61	8.32
ambigua	44.56	3.75	8.42	2.08	1.55	9.50	7.32
athabasca	34.24	3.19	9.32	1.20	1.12	6.95	6.42
azteca	53.44	5.93	11.10	3.12	2.68	11.76	9.80
bifasciata	41.08	4.53	11.02	2.12	1.54	10.43	7.78
bogotana	40.40	2.86	7.07	1.84	1.21	9.28	6.33
guanche	29.96	2.52	8.43	1.96	1.88	12.68	11.02
imaii	35.00	4.20	12.01	1.56	1.36	8.95	7.35
madeirensis	30.00	2.16	7.20	1.36	1.19	8.92	7.74
microlabis	32.24	2.86	8.88	1.92	1.75	11.80	10.24
miranda	41.20	3.69	8.95	2.08	1.32	10.14	6.37
narragansett	33.44	3.42	10.22	1.20	1.22	7.21	7.39
obscura	35.92	3.19	8.87	2.00	1.63	11.05	8.74
persimilis	38.52	3.25	8.45	1.96	1.43	10.26	7.43
pseudoobscura	47.04	3.34	7.09	2.40	2.06	10.03	8.40
subobscura	32.80	2.53	7.72	1.84	1.18	11.54	7.75
tolteca	36.92	3.13	8.49	2.04	1.79	10.86	9.30
tristis	43.88	6.73	15.35	3.08	2.04	14.31	9.69
mean	37.93	3.53	9.21	1.98	1.57	10.40	8.19
s.e.	1.51		2.11	0.12		0.43	

m, mean; s.d., standard deviation; CV, coefficient of variation; s.e, standard error;
FA-abs : absolute fluctuating asymmetry, i. e. mean of |L-R| individual values
FA-rel : relative fluctuating asymmetry : |L-R|/0.5 (L+R)

(ovarioles) the number of which is determined during early pupation, and can be counted without any measurement error in the adult female.

In a previous paper (Delpuech *et al.*, 1995) we failed to find any significant difference among isofemale lines of *D. melanogaster*, suggesting an absence of genetic variance for FA. It remained however possible that significant differences might occur over a much larger evolutionary time. We address this problem in the present paper, comparing FA among 18 species in a monophyletic clade, the *obscura* group in the *Sophophora* subgenus of *Drosophila*.

Basic data concerning ovariole number of 18 species are given in Table 1. Big variations of mean ovariole number (sum of both ovaries) were observed across species, with a maximum of 53.44 in *D. azteca* and a minimum of 29.96 in *D. guanche*. This trait, which is directly related to egg production and hence to fitness, is able to evolve rapidly and is not constrained by the phylogeny. A positive correlation was observed between mean value and standard deviation (r = 0.72). This correlation became non-significantly different from 0 (r = 0.38) when using the intraspecific coefficient of variation (CV), which on average, was 9.21 ± 2.11.

For analyzing FA, we first asked the question of a possible directional asymmetry, and pooled the values of 450 females (Figure 1A). In spite of a significant species heterogeneity, the overall distribution of the left minus right (L-R) difference was close to normality with a mean of 0.14 ±

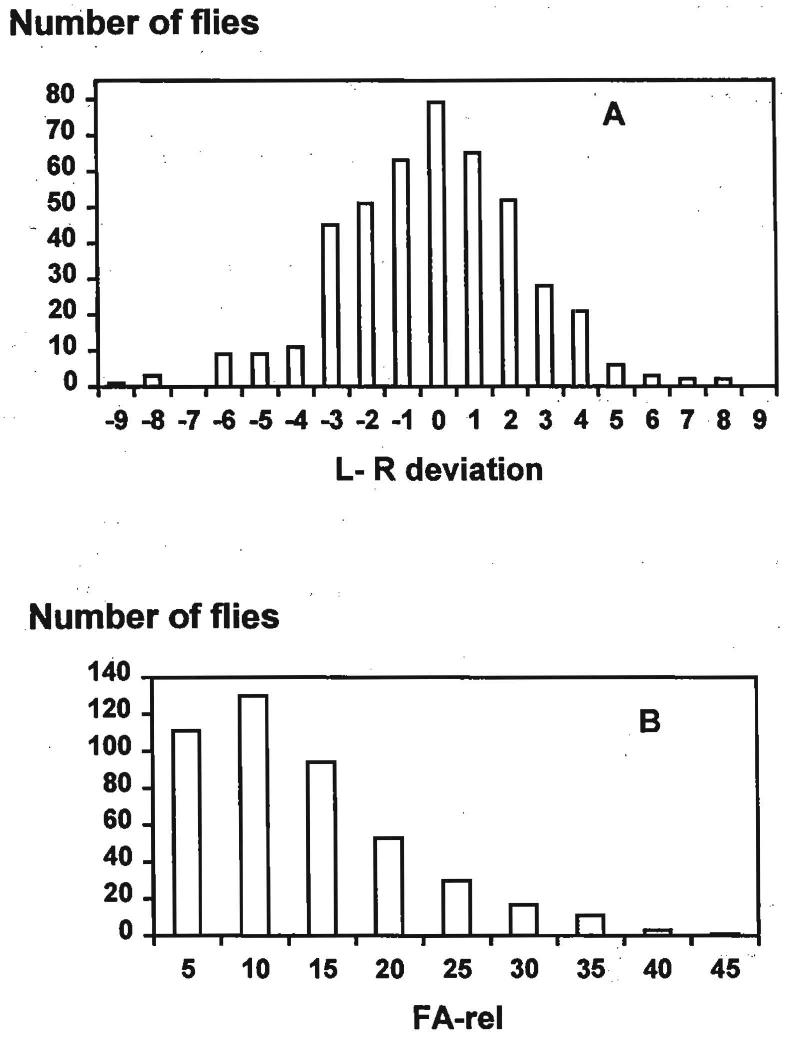

Figure 1. Distribution of ovarian fluctuating asymmetry among 450 females of the *D. obscura* species group. A, Distribution of the left (L) minus right (R) deviation (signed FA); B, Distribution of the relative fluctuating asymmetry (FA-rel) = 100|L-R|/0.5 (L+R).

0.12, very close to zero. There is apparently no trend for directional asymmetry in *Drosophila* ovaries and no departure from normality.

We then analyzed FA in each species, either by considering the absolute value |L-R| of the individual deviation (FA-abs) or by standardizing the deviation to the mean: FA-relative = (FA-rel) = 100|L-R|/0.5 (L+R) (see Table 1). Both estimates are classically used in FA investigations (Moeller and Swaddle, 1997). FA-abs was submitted to ANOVA and a significant species effect was found (p = 0.00067). Such a conclusion may be considered as valid in spite of the fact that the distribution of the variable |L-R| is truncated and far from normality (Gangestad and Thornhill, 1998). We also compared FA-abs with mean ovariole number and found a positive, highly significant correlation (r = 0.76) (Figure 2A). Such a correlation might be interpreted as a demonstration of significant differences across species. Standardizing the deviations to the mean number (FA-rel) provided however a different conclusion. ANOVA, applied to FA-rel failed to evidence any difference between species (p = 0.26). The correlation between mean number and FA also disappeared (Figure 2B) with a non-significant r = 0.17.

From these observations, we draw several conclusions. Firstly, a relative measurement of FA should be preferred in most investigations. This FA-rel, expressed in percent like a CV, will also permit a comparison of fluctuating asymmetry among different traits. Secondly, FA, at least for ovaries, seems to be a fairly stable trait, characteristic of *Drosophila*. In *D. melanogaster* the mean value for 30 isofemale lines was 10.17 ± 0.19 (Delpuech *et al.*, 1995) while it is 10.40 ± 0.43 for 18 species in the *D. obscura* group. Thirdly, it would be very interesting to know if, in other insect species, ovarian FA may be different from that observed in fruit flies.

Acknowledgments: We thank A.P. Moeller for helpful discussion on this paper.

References: Delpuech, J.M., B. Moreteau, J. Chiche, E. Pla, J. Vouidibio, and J. R. David 1995, Evolution 49: 670-675; Gangestad, S.W., and R. Thornhill 1998, Anim. Behav. 55: 497-501; Moeller, A.P., and J.P. Swaddle 1997, *Asymmetry, Developmental Stability, and Evolution.* Oxford University Press; Moeller, A.P., and R. Thornhill 1997, J. evol. Biol. 10: 69-76; Palmer, A.R., and C. Strobeck 1986, Ann. Rev. Ecol. Syst. 17: 391-421.

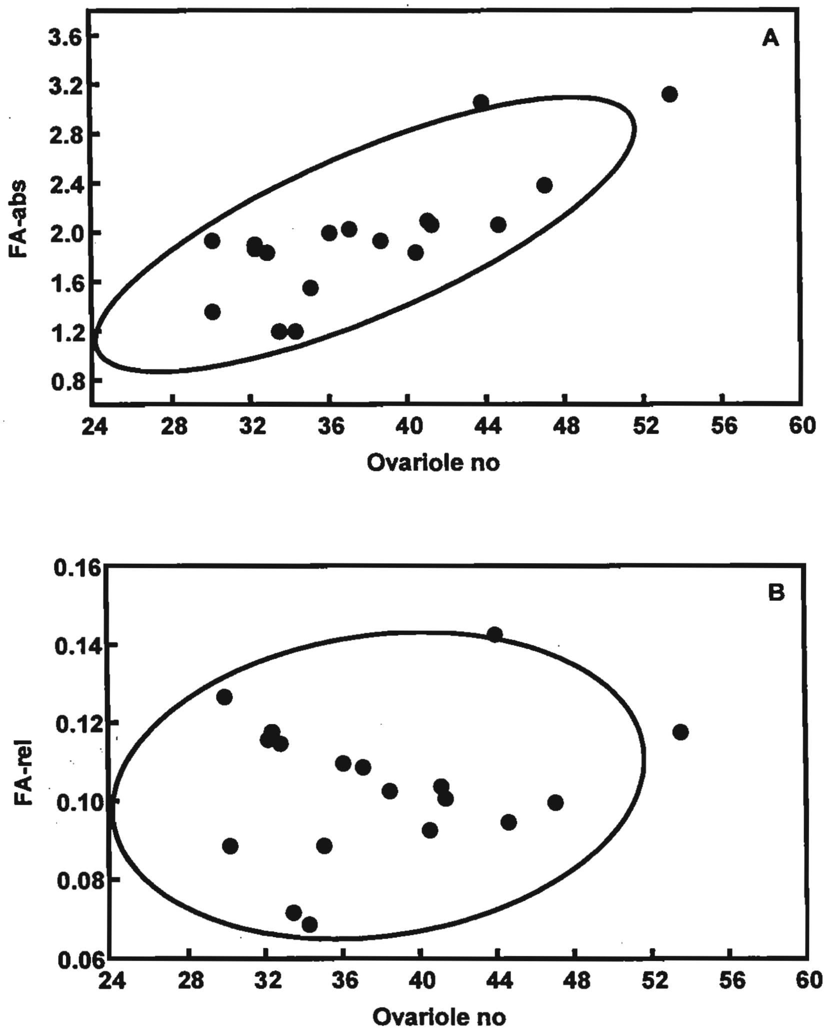

Figure 2. Relationship between ovariole number and FA. A, Positive correlation (r = 0.77) with absolute FA; B, Absence of correlation with relative FA (r = 0.17). Ellipses of 90% confidence are shown.

Effects of thermal stress on desert and cosmopolitan *Drosophila* behavior.

Weiss, Anne E. Department of Biology, Arizona State University, Tempe, AZ 85287-1501.

Abstract:

Organisms have variable responses to stress in their environment. Males from two *Drosophila* species, *D. mojavensis – Sonora SOSC0297* (desert) and *D. simulans – Tempe* (cosmopolitan), were tested for motor activity, mating behavior and offspring production following