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DOES INBREEDING AFFECTS DEVELOPMENTAL STABILITY IN *DROSOPHILA SUBOBSCURA* POPULATIONS *?*

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In the present paper, we focused on the coadaptive aspect of genetic variability at population level and its relation to genomic stress such as inbreeding. The paper evaluates the effects of an experimental reduction of average heterozygosity after fourteen generations of systematic inbreeding in laboratory conditions, on developmental stability in *Drosophila subobscura* populations from two ecologically and topologically distinct habitats, knowing that they possess a certain degree of genetic differences due to their different evolutionary histories. The aims were to analyze: (i) the variability change of wing size (length and width)

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among the inbred lines from both populations; (ii) the relations between homozigosity and level of fluctuating asymmetry as a potential measure of developmental instability, in inbred lines originating from two populations. Results for the wing size showed similar between line variability pattern across generations of systematic inbreeding in both populations. The obtained results suggest that variability of fluctuating asymmetry as a measure of developmental instability can not be related to homozygosity due to inbreeding *per se*, in both experimental populations.

Key words: fluctuating asymmetry, population, wing size

INTRODUCTION

Inbreeding, mating of close relatives, has commonly deleterious effects on fitness traits in organisms and increases the frequency of homozygotes in a population. The increased homozygosity of deleterious alleles will often lead to inbreeding depression – an average reduction of individual fitness – and thus might decrease the short-term viability in a population. Furthermore, the loss of heterozygosity, along with reduction in population size can compromise the evolutionary adaptive potential of a population, and thereby reduce the long-term viability of a population, especially in changing environments (FRANKHAM *et al.,* 2009; OUBORG *et al.,* 2010).

There is growing evidence that genomic stress can induce significant levels of developmental instability (DI) (PALMER and STROBECK, 1986; PALMER 1994, 1996; PERTOLDI *et al*., 2006a). Two principal methods are commonly used to estimate DI. Some studies used phenotypic variance of different morphological traits, where estimate can be blurred by the presence of genetic and/or environmental variability (ANDERSEN *et al.*, 2002; PERTOLDI *et al*., 2006a, b). Other studies used fluctuating asymmetry (FA), defined as small deviations from the perfect bilateral symmetry in morphological traits. Such dissimilarity in the expression of a given character on the left and right side cannot be explained either by genotypic or environmental differences, since the development of bilateral characters in an individual is ensured by the same genotype under identical environmental conditions (PALMER and STROBECK, 1986). Increased FA may occur for different genetic or environmental causes, including inbreeding and deleterious gene combinations. A number of studies have shown that DI is positively associated with the level of stress that individuals experience (PALMER, 1994; LENS *et al.*, 2002; PERTOLDI *et al*., 2006a). Disrupting the genetic composition of coadapted gene complexes by inbreeding (WALDMANN, 1999; SCHAEFER *et al*., 2006) or hybridization (KURBALIJA *et al.,* 2010), may increase the likelihood of developmental instability resulting in increased FA.

The heterozygosity theory predicts that levels of overall genomic heterozygosity will be inversely correlated with the level of DI (LERNER, 1954; LIVSHITS and KOBYLIANSKY, 1985; PERTOLDI *et al.*, 2006a). It has been suggested that heterozygosity has a buffering role through increased biochemical diversity, which enables a dynamic and stable developmental pathway in changing conditions

(LIVSHITS and SMOUSE, 1993). LERNER (1954) suggesting that heterozygosity in complex multi-genetics systems provides a mechanism for maintaining potential plasticity and promoting canalization.

A controversial issue is the ongoing discussion dealing with the overdominance hypothesis vs. the partial dominance hypothesis in explaining inbreeding depression. The first theory suggests that the capability to buffer biochemical pathways against negative genetic effects during ontogenesis is caused by a diversity of biochemical products resulting from heterozygous genotypes at unlinked loci. The later theory (partial dominance) explains heterozygote advantage with an increased expression of recessive deleterious alleles with increased homozygosity. When expressed, such rare deleterious alleles would be detrimental to metabolic processes (ROFF, 1998).

According to the overdominance hypothesis, fitness (biochemical efficiency) will always decrease with an increase in homozygosity. In consequence, DI would be expected to increase. However, with partial dominance, a decrease in fitness with decreased heterozygosity will not necessarily be observed because the deleterious alleles can be purged from the population. Therefore, with partial dominance, the association between DI and homozygosity may be very complex. Both the overdominance and the partial dominance hypotheses, however, predict enhanced growth and reduced DI at high levels of heterozygosity.

Drosophila subobscura is a Palaearctic species, which displays rich inversion polymorphism in all 5 acrocentric chromosomes of the set (KRIMBAS and LOUKAS, 1980, KRIMBAS, 1992; 1993). It is widely used as a suitable model system for studying processes involved in adaptation and genetic diversity. As crossing-over is suppressed within the inversion loops of heterokaryotypes, all genes within the inverted segments segregate as one physical and functional unit, called the 'supergene' (KRIMBAS, 1993). Assuming a relatively long-time of selection on the linked genes within inverted regions, DOBZHANSKY (1948) developed the coadaptation hypothesis, which proposed that the selective value of inversions depends on the combinations of alleles, genes and their interaction. The important aspect of this hypothesis is the effects of heterosis and fitness epistasis, causing the evolution of the genes evolve after their origin (HOFFMANN *et al.,* 2004).

In the present study, we evaluated the effects of an experimental reduction of average heterozygosity after fourteen generations of systematic inbreeding in laboratory conditions, on developmental stability in *Drosophila subobscura* populations from two ecologically and topologically distinct habitats, knowing that they possess a certain degree of genetic differences due to their different evolutionary histories. The following aims were to analyze: (i) the variability change of wing size (length and width) among the inbred lines from both populations; (ii) the relations between homozigosity and level of fluctuating asymmetry as a potential measure of developmental instability, in inbred lines originating from two populations.

MATERIALS AND METHODS

Population sample

For the present study *Drosophila subobscura* flies were collected at mountain Goc, situated between $43^0$33'-$43^0$35' N and $18^0$15'-18^0 40' E in Central Serbia. The local subpopulations were collected from two forest communities topographically about 6 km apart: Beech wood-B (*Abieto-fagetum*) and Oak wood-O (*Fraxineto-quercetum*), at about 800m above sea level. These two woods also have distinctive microclimates. Beech has higher humidity with great vegetation coverage. Oak has more sparse trees and is slightly warmer (GAJIC, 1984). These two populations were sampled using fermented fruit traps. Five IF lines were established from each population (B and O) and maintained under optimal laboratory conditions for this species (at 19 C, cca. 60% relative humidity, at light of 300 lux and 12/12 h light/dark cycles).

Experimental design and wing preparation

Randomly chosen couple of F1 progeny from each IF line represented parents of the first generation of full-sib (*FS*) mating. To minimize the loss of IF lines, additional 2-3 individual brother-sister mating were made within each line in every generation, but progeny of one pair was randomly chose to continue the experiment. Although this procedure allows natural selection to operate between additional matings within lines, it is used in most inbreeding studies (RUMBALL *et al*., 1994; PEGUEROLES *et al.,* 1996) to avoid excessive loss of lines and to reduce selection between lines (RUMBALL *et al*., 1994). For wing size analysis we used only males from the following groups: flies from F_1 generation collected from IF lines (F_1B and F_1O); flies from *FS* lines in 1. generation of inbreeding (F_{i1}B-1,…,5; F_{i1}O-1,…,5); flies from *FS* lines in 5. generation of inbreeding (F_{i5}B-1,…,5; F_{i5}O-1,…,5); flies from *FS* lines in 14. generation of inbreeding (F_{i14}B-1,…,5; F_{i14}O-1,…,5).

The left and right wings from each fly were cut and mounted on a slide using double-sided scotch tape and cover slip was placed over them. Each wing was photographed with a Canon Power Shot camera attached to a Leica stereomicroscope under 400x magnification. The measurements were performed on photographs, with Image Tool 3.0 (WILCOX *et al.*, 2002). (http://ddsdx.uthscsa.edu/dig/download.html).

The wing length was taken as a distance from the intersection of the third longitudinal vein (L3) with the anterior cross vein (A1) to the wing tip where the third vein ends. The wing width was taken as the distance between the ends of the second (L2) and the fifth longitudinal vein (L5) (as in KURABIJA *et al.,* 2010).

Statistical analysis

Before interpreting FA estimates, several statistical procedures were done. The measurement error was estimated for all samples by the two-way ANOVA on a sample of 30 individuals measured twice (PALMER, 1994). There were significant interactions between wing size and individual FA for both length (MS=1056.769, $p < 0.001$) and width (MS=557.514, $p < 0.001$) which means that FA has a grater value than the measurement error. The non-parametric tests, Shapiro–Wilk (W), were used

to test (R–L) for departures from normality. There are several available tests for normal distribution, and Shapiro–Wilk is high power test which is optimized for small sample sizes (N<50). The one-sample t-test was done to test a departure of the mean of (R–L) from the expected mean of zero. Test for presence of directional asymmetry (DA) was done, as the presence of DA artificially inflates the values of certain FA indices (PALMER, 1994). To test size dependence on the absolute FA, linear regression analyses of ((R+L)/2) on |R–L| were done for all samples.

The FA1 index (PALMER, 1994) of each trait was measured as the unsigned, |R–L| difference between sides in all inbreed lines, separately for Beech and Oak populations across generations. The FA1 index is one of the most frequently used indices to describe a level of FA in sample. It is also an unbiased estimator of the sample standard deviation (PALMER and STROBECK, 1992). Also, FA4 (PALMER, 1994) was used as the signed values of measures for both characters (wing length and width). FA4 index represents the variance of between sides differences for each individual (FA4=var(L-D)).

The F-test and t-test are commonly used tests if normal distributions are assumed. The F-test is for equal variance, while the t-test is for the equality of the means. These tests were conducted in order to test significant differences in the mean and variances of the wing length and width within lines between generations. All the statistical analyses were performed using PAST software (HAMMEMER *et al.*, 2001). Corrections for multiple comparisons were performed using overall Bonferroni correction (RICE, 1989).

RESULTS

Changes of the mean wing length and width in males from Beech and Oak populations are presented in Table 1. and Table 2., respectively. The mean value, in general, significantly increases from F1 to F5, and decreases in F14 in all IF lines, for both wing length and width. The same statistically significant pattern was found for both populations.

Fluctuating asymmetry

Before interpreting FA estimates, several statistical procedures were done. (deviations from normality, test of directional asymmetry and test for significant correlations between asymmetry and mean value of both traits). None of the samples show significant deviations from normality (the results are not shown) and the signed right-left (R–L) size analysis show that directional asymmetry (DA) is absent in all samples (the results are not shown). In less than 1% of the samples a positive correlation between |R–L| and the (R+L)/2 is found. After sequential Bonferroni correction, none of the regressions was significant, indicating that FA is not correlated with the trait size.

The results of differences in FA1 index between within IF lines from Beech and Oak populations between generations for the wing length and wing width after inbreeding are presented in Table 3. and Table 4., respectively. No significant differences in FA were found between generations within IF lines for both

populations, except of B1 line (F5>F14, t=2.04, t>0.05) and O1 for the wing length (F1>F14, t=2.5, p<0.05; F5>F14, t=2.42, p<0.05).

Table 1. The mean value of wing length and width of individuals from F1-F14 generations from Beech locality

line	character	generation	N	mean(L+D)/2±SE	*t test*	*p*
		F1	21	560.93±4.85	F1<F5, t=-6.17	***
	Length	F5	14	600.84±4.01	F1<F14, t=-4.74	***
B1		F14	31	585.95±2.88	F5>F14, t=3.15	*
		F1	16	361.27±2.80	F1<F5, t=-7.55	***
	Width	F5	14	384.60±2.23	F1<F14, t=-3.09	*
		F14	30	370.45±2.20	F5>F14, t=4.39	***
		F1	15	579.53±4.67	F1<F5, t=-7.67	***
	Length	F5	17	618.06±2.62	F1<F14, t=-3.13	*
B2		F14	13	598.41±3.59	F5>F14, t=4.40	***
		F1	15	367.13±2.87	F1<F5, t=-5.14	***
	Width	F5	16	383.92±1.92	F1<F14, t=-7.10	***
		F14	11	393.94±2.50	F5<F14, t=-3.52	*
		F1	30	597.70±2.96		
	Length	F5	14	617.28±3.66	F1<F5, t=-4.37	***
B3		F14	/			
		F1	30	382.82±2.34		
	Width	F5	14	400.58±2.54	F1<F5, t=-4.25	***
		F14	/			
		F1	14	566.70±4.84		
	Length	F5	16	622.57±3.21	F1<F5, t=-2.31	
B4		F14	/			
		F1	13	370.96±2.82		
	Width	F5	16	396.49±3.78	F1<F5, t=-5.14	***
		F14	/			
		F1	16	593.27±5.30	F1<F5, t=-10.29	***
	Length	F5	20	618.72±3.27	F1<F14, t=-0.52	
B5		F14	/		F5>F14, t=7.37	***
		F1	14	376.37±3.03	F1<F5, t=-4.82	***
	Width	F5	19	385.73±2.42	F1<F14, t=-1.92	
		F14	/		F5>F14, t=2.16	*

B1-B5 are isofemale lines; N-number of individuals; The values are presented in pixels.

p<0.05*, p<0.01**, p<0.001***

Table 2. The mean value of wing length and width of individuals from F1-F14 generations from Oak locality.

line	character	generation	N	mean(L+D)/2±SE	***t test***	***p***
		F1	29	562.34±4.79	F1<F5, t=-7.20	***
	Length	F5	26	608.88±4.24	F1<F14, t=-2.50	*
O1		F14	17	579.41±3.43	F5>F14, t=4.96	***
		F1	29	370.60±2.29	F1<F5, t=-6.65	***
	Width	F5	24	391.59±2.31	F1>F14, t=0.11	
		F14	17	370.25±1.77	F5>F14, t=7.08	***
		F1	14	591.67±6.41	F1<F5, t=-14.48	***
	Length	F5	23	629.01±2.20	F1<F14, t=-6.93	***
O2		F14	30	611.26±4.13	F5>F14, t=6.08	***
		F1	12	364.26±3.38	F1<F5, t=-14.62	***
	Width	F5	/	408.22±2.01	F1<F14, t=-8.86	***
		F14	27	371.72±2.16	F5>F14, t=7.62	***
		F1	20	582.43±4.19		
	Length	F5	/		F1<F14, t=0.39	
O3		F14	17	591.19±4.15		
		F1	16	369.93±3.28		
	Width	F5	/		F1<F14, t=0.12	
		F14	16	382.93±1.56		
		F1	/			
	Length	F5	23	629.01±2.34	F5>F14, t=4.37	***
O4		F14	20	601.55±4.03		
		F1	/			
	Width	F5	23	408.21±1.23	F5>F14, t=1.81	
		F14	20	393.84±1.45		
		F1	25	562.82±3.82		
	Length	F5	/		F1<F14, t=-1.47	
O5		F14	18	595.11±4.56		
		F1	22	365.39±2.69		
	Width	F5	/		F1<F14, t=-3.20	*
		F14	21	381.35±2.89		

O1-O5 are isofemale lines; N-number of individuals; The values are presented in pixels.

Table 3. The results of FA1 index for wing length and width in individuals from F1-F14 generations from Beech locality

line	character	generation	N	FA1=mean|L-D|±SE	***t test***	***p***
		F1	21	4.51±0.73	F1<F5, t=-1.44	
	Length	F5	14	6.13±1.09	F1>F14, t=0.34	
B1		F14	31	4.21±0.50	F5>F14, t=2.04	*
		F1	16	3.14±0.58	F1<F5, t=-0.43	
	Width	F5	14	3.44±0.75	F1<F14, t=-1.04	
		F14	30	3.78±0.41	F5<F14, t=-0.39	
		F1	15	3.55±0.81	F1<F5, t=-0.05	
	Length	F5	17	3.72±1.00	F1<F14, t=-0.39	
B2		F14	13	4.07±1.07	F5<F14, t=-0.31	
		F1	15	2.81±0.56	F1<F5, t=-0.50	
	Width	F5	16	3.19±0.69	F1<F14, t=-0.22	
		F14	11	3.20±0.78	F1<F14, t=-0.12	
		F1	30	3.84±1.01		
	Length	F5	14	5.59±0.82	F1<F5, t=-0.93	
B3		F14	/			
		F1	30	3.09±0.61		
	Width	F5	14	4.19±0.68	F1<F5, t=1.23	
		F14	/			
		F1	14	3.28±0.61		
	Length	F5	16	5.66±1.78	F1<F5, t=-0.17	
B4		F14	/			
		F1	13	2.62±0.59		
	Width	F5	16	3,61±1.31	F1<F5, t=0.82	
		F14	/			
		F1	16	4.38±0.85		
	Length	F5	20	3.21±0.63	F1>F5, t=0.93	
B5		F14	/			
		F1	14	4.60±0.90		
	Width	F5	19	3.04±0.53	F1>F5, t=1.5	
		F14	/			

B1-B5 are isofemale lines; N-number of individuals; The values are presented in pixels.

p<0.05*, p<0.01**, p<0.001***

Table 4. The results of FA1 index for wing length and width in individuals from F1-F14 generations from Oak locality.

line	character	generation	N	FA1=mean|L-D|±SE	*t test*
		F1	29	5.09±0.66	F1>F5, t=0.30
	Lenght	F5	26	4.82±0.62	F1>F14, t=2.5
O1		F14	17	2.76±0.46	F5>F14, t=2.42
		F1	29	4.55±0.52	F1>F5, t=1.43
	Width	F5	24	3.68±0.76	F1>F14, t=1.04
		F14	17	3.55±0.67	F5>F14, t=1.02
		F1	14	5.00±0.98	F1>F5, t=1.45
	Lenght	F5	23	4.98±0.80	F1<F14, t=-1.27
O2		F14	30	5.35±0.84	F5<F14, t=-0.08
		F1	12	5.11±1.81	
	Width	F5	/		F1>F14, t=-0.95
		F14	27	4.78±0.68	
		F1	20	3.17±0.48	
	Lenght	F5	/		F1<F14, t=-0.11
O3		F14	17	3.66±0.65	
		F1	16	3.45±0.75	
	Width	F5	/		F1>F14, t=0.35
		F14	16	3.14±0.59	
		F1	/		
	Lenght	F5	23	5.22±0.78	F5>F14, t=0.11
O4		F14	20	5.07±0.97	
		F1	/		
	Width	F5	23	4.06±0.81	F5>F14, t=0.88
		F14	20	3.65±0.61	
		F1	25	3.67±0.60	
	Lenght	F5	/		F1>F14, t=0.62
O5		F14	18	3.46±0.72	
		F1	22	4.08±0.74	
	Width	F5	/		F1>F14, t=0.53
		F14	21	2.70±0.43	

O1-O5 are isofemale lines;N-number of individuals; The values are presented in pixels.

p<0.05*, p<0.01**, p<0.001***

Table 5. The results of FA4 index of wing length and width in individuals from F1-F14 generations from Beech locality.

line	character	generation	N	FA4 = var(L-D)	*F test*
B1	Lenght	F1	21	32,270	F1<F5, F=1.43
		F5	14	38,678	F1>F14, F=1.46
		F14	31	24,337	F5>F14, F=1.89
	Width	F1	16	14,967	F1<F5, F=1.39
		F5	14	20,494	F1<F14, F=1.34
		F14	30	19,314	F5>F14, F=1.06
B2	Lenght	F1	15	19,612	F1<F5, F=1.39
		F5	17	30,763	F1<F14, F=1.45
		F14	13	28,477	F5>F14, F=1.41
	Width	F1	15	13,215	F1<F5, F=1.47
		F5	16	18,502	F1<F14, F=0.81
		F14	11	14,568	F5>F14, F=1.38
B3	Lenght	F1	30	17,097	
		F5	14	22,622	F1<F5, F=1.08
		F14	/		
	Width	F1	30	15,172	
		F5	14	20,371	F1<F5, F=2.03
		F14	/		
B4	Lenght	F1	14	13,081	
		F5	16	12,492	F1>F5, F=0.24
		F14	/		
	Width	F1	13	9,786	
		F5	16	9,510	F1>F5, F=0.33
		F14	/		
B5	Lenght	F1	16	23,094	
		F5	20	19,536	F1>F5, F=0.33
		F14	/		
	Width	F1	14	21,784	
		F5	19	15,108	F1>F5, F=0.77
		F14	/		

B1-B5 are isofemale lines; N-number of individuals; The values are presented in pixels.

$p<0.05$*, $p<0.01$**, $p<0.001$***

Table 6. The results of FA4 index for wing length and width in individuals from F1-F14 generations from Beech locality

line	character	generation	N	FA4 = var(L-D)	*F test*	*p*
		F1	29	38,968	F1>F5, F=1.39	
	Length	F5	26	28,258	F1>F14, F=3.51	*
O1		F14	17	11,207	F5>F14, F=2.52	
		F1	29	27,305	F1>F5, F=1.26	
	Width	F5	24	26,841	F1>F14, F=1.19	
		F14	17	20,825	F5>F14, F=1.5	
		F1	14	35,212	F1>F5, F=1.06	
	Length	F5	23	30,261	F1<F14, F=1.40	
O2		F14	30	44,336	F5<F14, F=1.14	
		F1	12	37,754		
	Width	F5	/		F1>F14, F=1.23	
		F14	27	34,818		
		F1	20	15,013		
	Length	F5	/		F1<F5, F=1.09	
O3		F14	17	19,239		
		F1	16	20,735		
	Width	F5	/		F1>F14, F=1.21	
		F14	16	14,339		
		F1	/			
	Length	F5	23	40,691	F5>F14, F=1.01	
O4		F14	20	32,301		
		F1	/			
	Width	F5	23	32,398	F5>F14, F=1.27	
		F14	20	21,598		
		F1	25	23,041		
	Length	F5	/		F1>F14, F=1.28	
O5		F14	18	18,996		
		F1	22	29,361		
	Width	F5	/		F1>F14, F=1.59	
		F14	21	21,383		

O1-O5 are isofemale lines; N-number of individuals; The values are presented in pixels.

p<0.05*, p<0.01**, p<0.001***

The results of differences in FA4 index between within IF lines from Beech and Oak populations between generations for the wing length and wing width after inbreeding are presented in Table 5. and Table 6., respectively. No significant difference in FA was found between generations within IF lines in any of

populations, except of O1 line, with significant increases of wing length FA in F14 generation compared to F14 generation ($F=3.51$, $p<0.05$)

DISCUSSION

In the present paper, we focused on the coadaptive aspect of genetic variability at population level and its relation to genomic stress such as inbreeding in two *Drosophila subobscura* populations. Previous analyses of the genetic variability parameter such as inversion polymorphism showed that two presently analyzed populations differ in the frequencies of some gene arrangements (ANDJELKOVIC *et al.,* 2003; STAMENKOVIC-RADAK *et al.,* 2008; KURBALIJA NOVICIC *et al.,* 2011). The results suggested that different gene arrangements are carriers of various alleles that are differently favored in diverse environmental conditions and prove in most cases to be the major factor determining the gene arrangement frequencies in natural populations of *D. subobscura* (ANDJELKOVIC *et al.,* 2003). RASIC *et al.* (2008) also showed that the genetic systems of the beech and oak populations differ to a certain degree in the structurality and integrity of the genome. The results also suggested that increase of the homokaryotype frequency over generations of inbreeding per chromosome is population specific. Furthermore, KURBALIJA *et al.* (2010) confirmed particular structure and integrity of the genome for each population on phenotypic level and suggested that the associations between coadaptive genes with the same evolutionary history are the most probable mechanism that maintains the developmental homeostasis in *Drosophila subobscura* populations.

Our results for the wing size showed similar between line variability pattern across generations of systematic inbreeding in both populations. The mean size, in general, significantly increases from F1 to F5, and decreases in F14 in all inbred lines, for both wing characters. According to literature, inbreeding leeds to increased differences in wing size among inbred lines because of the fact that genetic variance is distributed more between lines than within lines (FALCONER and MACKAY, 1996) and because inbreeding tends to increase the environmental variance between inbred lines (KRISTENSEN *et al*., 2005).

Many studies have investigated the association between asymmetry, decreased heterozigosity or disruption of coadapted gene complexes (MARKOW, 1995). In our experiment, we expected that systematic inbreeding across 14 generation destroys favored gene complex interactions in homokariotype genome with higher probability of recombination, and thus the effects on individual fitness as increase of developmental instability (measured as FA). However, the obtained results suggest that variability of fluctuating asymmetry (FA) as a measure of developmental instability can not be related to homozygosity due to inbreeding *per se*, in both experimental populations. The possible explanation is that by increasing homozygosity and thus, by exposing recessive genes, inbreeding can improve the effectiveness of selection against deleterious mutations, both within inbred families and through extinction of inbred lines (HEDRICK, 1994; ROFF, 2002). This phenomenon of 'purging of inbreeding depression' is especially effective in the case of genes of major effect, such as recessive lethals and sub-lethals (HEDRICK, 1994;

WILLIS, 1999). Our results are not consisted with those obtained in studies with plants or other mammal species that have reported higher FA in inbred or more homozygous populations (WALDMANN, 1999; SCHAEFER *et al.,* 2006). It is clear that inbreeding may have different effects on developmental stability in different populations and species under different experimental conditions, as well (LENS *et al.,* 2000). Additional study should be performed to address the relationship between FA and inbreeding depression. Such a measure of developmental instability as FA needs to be used with caution as a biomarker in natural populations under inbreeding.

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DA LI INBRIDING UTIČE NA RAZVOJNU STABILNOST U POPULACIJAMA *DROSOPHILA SUBOBSCURA?*

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I z v o d

Rad je fokusiran na ko adaptivni aspekt genetičke varijabilnosti na nivou populacije i u odnosu na genomski stres kao što je inbriding. Analizirani su efekti eksperimentalnog smanjenja prosečne heterozigotnosti nakon 14 generacija sistematskog inbridinga u laboratorijskim uslovima na razvojnu stabilnost *Drosophila subobscura* populacija sa dva ekološki i topološki odvojena staništa, znajući da one poseduju odredjeni stepen genetičke diferencijacije usled različitih evolutivnih istorija. Ciljevi rada su bili da se analizira: (i) varijabilnost u promeni veličine krila (dužine i širine) medju inbidingovanim linijama i populacijama; (ii) odnosi izmedju homozigotizacije i nivoua fluktuirajuće asimetrije kao potencijalne mere razvojne nestabilnosti u inbridingovanim linijama obe populacije. Rezultati veličine krila pokazuju sličnu varijabilnost medju linijama obe populacije kroz generacije inbridinga. Dobijeni rezultati sugerišu da varijabilnost fluktuirajuće asimetrije kao mere razvojne nestabilnosti ne mogu biti povezani sa homozigotizacijom usled inbridinga *per se*, u obe eksperimentalne populacije.

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