

B chromosomes and developmental homeostasis in the yellow-necked mouse, *Apodemus flavicollis* (Rodentia, Mammalia): Effects on nonmetric traits

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B chromosomes are found in almost all populations of the yellow-necked mouse, *Apodemus flavicollis* (Rodentia, Mammalia). Their effects on developmental homeostasis in this species were analyzed using morphological nonmetric traits (number of foramina) in a sample of 218 animals from locality Mt Jastrebac in the former Yugoslavia. Variations of the parameters of developmental homeostasis (the degree of fluctuating asymmetry – FA, the number of asymmetrical characters per individual – NA, and the total phenotypic variability – PV) were examined in three groups: in animals without Bs, with one B chromosome, and with more than one B chromosome. Significant differences in the level of FA between groups of animals were found for two characters. Carriers of one B chromosome displayed the highest level of

phenotypic variability. Parameters of developmental stability (DS) were monitored in the population in which significant variations in the frequency of animals with Bs (fB) were established during the season earlier. The FA levels for four foramina out of a total of 12 examined followed the changes of frequencies of animals with Bs. Furthermore, a significant seasonal correlation between NA and fB was found. The presence of B does not cause a disturbance of homeostasis in a way that allows changes in homeostasis to be directly related to B chromosome's presence. However, carriers of B react differently to environmental changes than do non-carriers.

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Introduction

B chromosomes (Bs) are accessory genomic elements that occur in many species, from all the major taxonomic groups except birds. It is widely accepted that they originate from A chromosomes, although other possibilities have been suggested (Camacho *et al*, 2000). Their dispensable nature is the only property that is shared by all Bs. Other features, including non-Mendelian inheritance, heterochromatinization, a different morphology relative to A chromosomes, and nonpairing with As, although common, are properties that are not shared by all Bs (Jones and Rees, 1982; Vujošević, 1993).

Despite many attempts to link them with phenotypic and environmental variations, the adaptive significance of Bs in populations is largely unknown. In mammals, Bs are found in about 50 species. The effects of their presence on population biology are not understood (Vujošević, 1993). Bs are common in the yellow-necked mouse, *Apodemus flavicollis* (Soldatovic *et al*, 1975; Kral *et al*, 1979; Giagia *et al*, 1985; Sablina *et al*, 1985; Vujošević *et al*, 1991; Nadjafova *et al*, 1993; Boeskorov *et al*, 1995 and Zima and Macholán, 1995). Molecular markers that are unique to the DNA of Bs were demonstrated in this species (Tanic *et al*, 2000). Substantial differences in the

frequencies of B carriers were observed between different populations (Vujošević *et al*, 1991; Vujošević and Blagojević, 1994; Zima and Macholán, 1995). In this species, constant, apparently equilibrium frequencies of Bs were observed in the course of 8-year studies, notwithstanding the changes in population density (Vujošević, 1992; and unpublished data). However, significant seasonal alterations in the frequencies of animals with Bs were found when stress was caused by overcrowding (Blagojevic and Vujošević, 1995). In the absence of such stress, seasonal changes of the frequencies of animals with Bs were not significant (Vujošević and Blagojević, 1995). Furthermore, it was established that the frequency of animals with Bs positively correlated with the average number of subzero temperature days and negatively with the number of days when the daily temperature was close to the expected average. Thus, the frequencies of animals with Bs are highest under extreme climatological conditions (Vujošević and Blagojevic, 2000). Furthermore, it was observed that the presence of Bs in this species affected certain morphometric traits (Blagojevic and Vujošević, 2000). All of these findings indicate that the presence of Bs in populations of *A. flavicollis* may influence its population dynamics.

Information concerning the effects of Bs on growth and development is mainly based on studies in plants. In general, depending on the number of Bs, their effects are either neutral or deleterious. Advantages to individuals or populations have been found in a few cases only (Jones and Rees, 1982). It has been found that cellular and nuclear volumes positively correlate with the

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amount of DNA, which is increased by the presence of Bs. Important life history features, such as the rates of cell division, development, and metabolism, are influenced by this relationship (Gregory and Hebert, 1999). Changes in genome size that are produced by Bs can be the subject of natural selection.

The measurement of the levels of fluctuating asymmetry (FA) is an approach that can be used to study the potential effects of Bs on development. FA represent small, random, and nondirectional departures from the ideal symmetry of a bilaterally symmetrical trait (Ludwig, 1932). It is frequently used as a measure of the developmental stability (DS), which is defined as the ability of an organism to develop the same phenotype under given environmental conditions (Mather, 1953). Developmental stability can be disturbed by both environmental and genetic factors. Increasing numbers of investigations use changes in the FA as a measure of environmental quality (Clarke and McKenzie, 1987; McKenzie and Clarke, 1988; Zakharov and Yablokov, 1990; Pankakoski *et al*, 1992; Øxnevad *et al*, 1995; Auffray *et al*, 1999). FA has been shown to be a good statistic for characterizing the state of a population (Leary and Allendorf, 1989; Zakharov *et al*, 1991; Zakharov and Graham, 1992).

Both metric and meristic characteristics could be used to evaluate FA. However, meristic traits are more reliable, due to the negligible error in counting. It has been established that meristic characteristics are influenced by environmental factors (Searle, 1954; Berry and Searle, 1963; Berry, 1968; Self and Leamy, 1978).

The aim of this work was to investigate any relationship between the presence of Bs and developmental homeostasis.

Materials and methods

Specimens of yellow-necked mice were sampled from locality Mt Jastrebac (UTM: EP-30) during 1989. A total of 247 animals were collected when the seasonal variability in the frequency of specimens with Bs (fB) was studied (March fB=0.40, April fB=0.53, May fB=0.29, June fB=0.40, September–October fB=0.50; for more details, see Blagojević and Vujošević, 1995).

Foramina are small openings in the skull for nerves and blood vessels. Paired foramina on the cleaned skull under a dissecting binocular microscope (magnification $\times 16$) were counted. In all, 12 foramina on the skull and mandible were scored according to Larina and Eremina (1988): Fsf – foramen squamae frontalis; Fs – foramen squamosis; Fd – foramen diastemae; Fpal – foramen palatinum; Fh – foramen hypoglossum; Foa – foramen orbitalis anterior; Fos – foramen orbitalis superior; Fam – foramen alveolaris maxillaris; Fas – foramen alisphenoideum; Fas – foramen ovale; Fm – foramen mentale; and Fmb – foramen mentale b. The foramina were counted without any prior knowledge of the presence or absence of Bs in the respective animals. Furthermore, they were counted and double-checked by one person (JB). Damaged skulls were discarded, so, in total, 218 skulls were analyzed (March $N=47$, April $N=81$, May $N=64$, June $N=14$ and September–October $N=12$).

For each foramen pair, DA was assessed by the signed differences between sides (Palmer, 1994). All DA values were summarized to give a character DASUM that was

useful as an overall indicator of DA (Leamy *et al*, 1998). The level of DA was tested by the paired *t*-test. All probabilities generated in these tests were estimated for significance by the sequential Bonferroni procedure (Rice, 1989). To rule out the presence of antisymmetry (*R-L*), values and DASUM were tested for skewness and kurtosis. The significance of the dependence of FA on size was tested by linear regression of *R-L* on body length (measured by a caliper with 0.5 mm accuracy). FA was defined by absolute differences between sides (FA1) (Palmer and Strobeck, 1986). FASUM was obtained by adding all individual FA scores (Leamy *et al*, 1998) for each of 12 foramina. Groups without (0B), with one (1B), and with more than one ($>1B$) Bs were compared by the Levene test (the significance was evaluated by the sequential Bonferroni procedure).

Another measure of developmental homeostasis was the mean number of asymmetrical characters per individual (NA) (Leary *et al*, 1983) and the total phenotypic variability PV (Soulé, 1982; Pankakoski *et al*, 1987). The total phenotypic variability of the foramina was calculated as $PV = \text{Var}(R + L)$.

In order to compare the NA between groups or during a particular season, one-way ANOVA was used. The medians of the variance (PV) were compared with Fridman's nonparametric test.

Results

In order to examine the effects of Bs on developmental stability, three groups were formed: (i) without Bs (comprising 57.8% of the total sample), (ii) with one B chromosome (31.7%), and (iii) with more than one B chromosome (10.5%). The last group consisted of animals with two Bs (82.6%), three Bs (13.1%), and five Bs (4.3%). The sex ratio was close to 1:1 in all groups.

As recommended by Soulé (1967), a paired *t*-test was used to determine the significance of DA for 12 foramina analyzed and DASUM for each group separately (Table 1). To avoid type I error, the Bonferroni procedure was applied. No significant differences were detected. Differences between sides tended to be positive in sign (right side larger than the left) in all groups. Also, none of the skewness or kurtosis statistics calculated for (*R-L*) for all foramina or DASUM was statistically significant in the sequential Bonferroni tests.

Regression $|R-L|$ against body length was performed in order to eliminate the size dependence of FA within samples. In all three groups, no significant levels of association were detected for any of the foramina.

The level of FA was expressed as unsigned differences (Table 2). Significant differences between groups were found for two foramina (Fst and Fs). For foramen Fst, the lowest level of FA was found in the group of animals with 1B, while the level of FA for Fs was decreasing with increased number of Bs. The overall level of FA (FASUM) was not significantly different between groups.

The mean number of asymmetrical foramina (NA) was 5.43 in the group of animals without Bs, 5.13 in the group of animals with one B, and 5.35 in the group of animals with more than one B chromosome. The difference between the analyzed groups was not significant ($F_{(2,215)} = 0.49$). The total phenotypic variability (PV) of the foramen numbers is presented in Table 3. The groups

Table 1 Indexes of DA (\pm SE) in three groups: without B chromosomes (0B), with one B (1B) and with more than one B chromosome (>1B)

Foramen	0B (N = 126)		1B (N = 69)		>1B (N = 23)	
	Mean \pm SE		Mean \pm SE		Mean \pm SE	
Fsf	+0.111	0.049	-0.014	0.053	+0.043	0.117
Fs	-0.008	0.043	-0.014	0.048	+0.043	0.043
Fd	+0.151	0.081	+0.014	0.119	0.000	0.154
Fpal	0.000	0.084	+0.072	0.093	+0.522	0.207
Fh	-0.135	0.060	+0.203	0.087	+0.043	0.117
Foa	+0.175	0.067	+0.217	0.107	+0.217	0.140
Fos	+0.095	0.067	+0.275	0.111	+0.043	0.160
Fam	-0.103	0.104	-0.058	0.143	-0.391	0.233
Fas	-0.024	0.078	+0.072	0.124	-0.261	0.157
Fov	+0.016	0.080	-0.029	0.099	-0.130	0.158
Fm	+0.095	0.105	-0.058	0.130	+0.174	0.279
Fmb	-0.000	0.091	+0.116	0.131	-0.087	0.198
DASUM	+0.373	0.261	+0.497	0.395	+0.217	0.499

Table 2 Indexes of FA in three groups: without B chromosomes (0B), with one B (1B) and with more than one B chromosome (>1B) and results of the Levene test

Foramen	FA = R-L			Levene test		$F_{(2,215)}$	P-value(*)
	0B (N = 126)	1B (N = 69)	>1B (N = 23)	MS Effect	MS Error		
	Fsf	0.302	0.188	0.304	0.339		
Fs	0.183	0.159	0.043	0.475	0.085	5.607	0.048
Fd	0.595	0.652	0.435	0.121	0.121	0.995	ns
Fpal	0.651	0.478	0.783	0.142	0.096	1.473	ns
Fh	0.405	0.464	0.304	0.113	0.046	2.459	ns
Foa	0.444	0.594	0.478	0.103	0.082	1.262	ns
Fos	0.429	0.565	0.478	0.325	0.115	2.818	ns
Fam	0.937	0.913	0.870	0.063	0.335	0.188	ns
Fas	0.563	0.623	0.522	0.334	0.115	2.916	ns
Fov	0.587	0.522	0.391	0.046	0.093	0.499	ns
Fm	0.698	0.580	0.870	0.276	0.097	2.843	ns
Fmb	0.683	0.696	0.696	0.261	0.176	1.482	ns
FASUM	6.476	6.435	6.174	1.270	2.420	0.525	ns

(*)P values after sequential Bonferroni correction. ns = nonsignificant.

Table 3 Level of phenotypic variability (PV \times 10) of foramen number in the three studied groups: without B chromosomes (0B), with one B (1B) and with more than one B chromosome (>1B)

Foramen	0B	1B	>1B
Fsf	0.88	0.89	1.11
Fs	0.89	0.92	0.91
Fd	3.46	4.63	2.57
Fpal	6.00	6.35	8.38
Fh	2.38	2.62	4.03
Foa	2.31	2.96	2.83
Fos	2.07	2.23	2.11
Fam	9.78	6.11	3.28
Fas	5.00	6.62	3.09
Fov	3.07	4.05	2.60
Fm	6.52	7.77	5.89
Fmb	9.15	11.69	6.34
Median	1.58	2.67	1.75

differed significantly in the level of PV ($\chi^2_{(12,2)} = 8.17$, $P < 0.02$). The group of animals with one B chromosome had the highest, while the group of animals without Bs

had the lowest average level of PV for the analyzed foramina.

At the Mt Jastrebac locality during the year of investigation, the change of frequency of specimens with Bs that was monitored from March to October displayed significant differences in frequency between sampling times (Blagojević and Vujošević, 1995). For all 12 foramina, seasonal variations in the level of the FA were analyzed and compared with the variation in the frequency of animals with Bs. For four foramina, the level of the FA mostly followed changes in the frequency of animals with Bs (Figure 1a), but without any statistical significance. This was the consequence of the differences that were displayed by the last two samples. It should be noted that these four foramina show a statistically significant decrease in the level of the FA, from April to May sample, which correlated with the changes of fB. The number of asymmetrical foramina (NA) was examined. The number of asymmetrical foramina ($F_{(4,229)} = 3.96$, $P < 0.005$) also exhibited seasonal variations. The correlation between the frequency of animals with Bs and the number of asymmetrical foramina was statistically significant $r = 0.91$, $P < 0.05$ (Figure 1b).

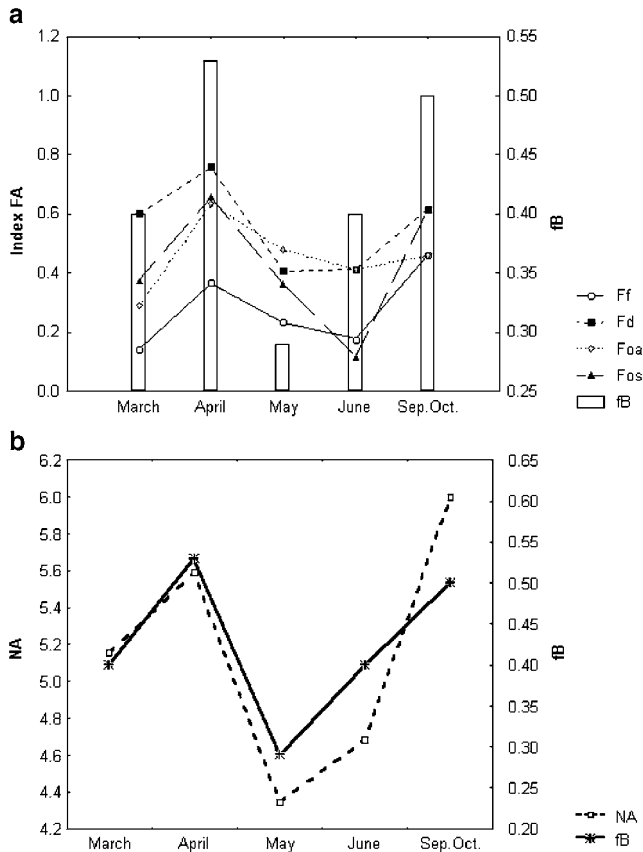


Figure 1 (a) Relationship between the indices of fluctuating asymmetry for four foramina and fB during the season. (b) Seasonal changes in the number of asymmetric foramina (NA) and fB during the season.

Discussion

The effects of Bs on development are not well known, especially in animals (Jones and Rees, 1982). In males of the grasshopper, *Myrmeleotetix maculatus* (Hewitt and East, 1978), development is slower in the presence of more than one B chromosome. The presence of Bs in males of the mealy bug, *Pseudococcus obscurus*, reduces the rate of development and number of spermatozoa (Nur, 1969). The most probable mode by which Bs affect development is by increasing the amount of genetic material, which in turn affects the duration of cell division. These theoretical expectations were confirmed in plants (Evans *et al.*, 1972).

Skull foramina are morphological structures whose bilateral symmetry probably bears no importance for the fitness of an organism. Thus, they are very useful in investigations of developmental homeostasis. The prenatal period is critical for the development of skull foramina (Zakharov *et al.*, 1991). The unchanging environment during intrauterine development decreases the effects of external environmental variations (Novak *et al.*, 1993). Prolonged development in perturbed environments increases the effects of stress.

In general, analysis of our results revealed that differences in the levels of FA between different groups of animals (in specimens without, with one and with

more than one B chromosome) are small and without any obvious trend.

Significant differences in phenotypic variability among the groups analyzed point to the possibility of differential effects of natural selection under adverse environmental conditions. The group of animals with one B chromosome possesses a higher level of phenotypic variability. Our previous results showed that under conditions of overcrowding, animals with one B chromosome were preferentially eliminated from the population (Blagojević and Vujošević, 1995). The increase of the PV in this group could explain preferential selection. The observed differences, although not very pronounced, were nevertheless not negligible.

The number of asymmetrical foramina (NA) is negatively correlated with developmental homeostasis. Namely, a decrease of developmental homeostasis was accompanied by an increase of the average number of asymmetrical foramina. The differences in the NA between animals with and without Bs were not significant. However, when seasonal changes were considered, variation of the NA significantly correlated with the frequency of specimens possessing Bs. The levels of the FA in one-third of the foramina analyzed followed the changes in frequency of animals with Bs in a similar manner. This trend was significant when the first three seasonal samples, which were large, were considered. Two explanations are possible: (i) specimens with Bs had a lower level of developmental stability; thus, an increase in the frequency of these specimens in the population was accompanied by decreased developmental homeostasis; and (ii) environmental factors influenced both developmental homeostasis and the frequency of animals with Bs.

The frequency of animals with Bs was positively correlated with the population density on Mt Jastrebac (Blagojević and Vujošević, 1995). Carriers of one B chromosome were preferentially eliminated from the population under conditions of stress produced by overcrowding. Zakharov *et al.* (1991) established a positive correlation between population density and developmental homeostasis in the cyclic population of *Sorex araneus* in Siberia. It is assumed that population density is an important negative factor that affects pregnant females. Our results also point to the population density as a significant factor in the variation in the frequency of specimens with Bs and simultaneous developmental homeostasis.

In the case of *A. flavicollis*, a relationship between environmental variation and DS obviously exists. However, a relationship between genetic variation resulting from the presence of Bs and DS could not be established. Similar results were obtained in the superspecies of the mole rat *Spalax ehrenbergi* (Auffray *et al.*, 1999). This species is represented by five chromosomal species in the Near East. It was established that the levels of DS were very heterogeneous between different populations (presumably due to environmental effects), but did not differ between species (with different genetic effects). The authors concluded that when natural populations are studied, in the determination of developmental stability, the complementary effects of both the environment and of genomes should be considered.

The relationship between developmental stability and the functional structure of the genome, that is, its

chromosomal organization, is not clear. Chatti *et al* (1999) found that Robertsonian fusions in *Mus musculus* could produce developmental instability. Yet, in the same species, Auffray *et al* (2001) found that a single stable or spontaneous balanced structural rearrangement (Robertsonian fusions) did not cause a disturbance in developmental stability.

The presence of Bs, by itself, does not disturb homeostasis in a manner that could be explicitly assigned to their presence. Nevertheless, carriers of Bs react differently to environmental changes than do noncarriers. The presence of Bs expands the genetic variability of populations of *A. flavicollis*, allowing this species to be less vulnerable to environmental changes.

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