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SEX-RATION IN A NATURAL POPULATION OF *DROSOPHILA SUBOBSCURA* FROM MOUNTAIN GOČ, SERBIA

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The results given in this paper represent the analysis of the ratio of sexes in the offspring of the wild males and females of a *D. subobscura* natural population collected at mountain Goč, Serbia, during two successive years. The analysis of the departure from 1:1 ratio and the k-values obtained, show that sex-ratio is balanced in the population studied.

KEY WORDS: *Drosophila*, sex-ratio, natural population.

INTRODUCTION

It is well known that there are equal numbers of individuals of both sexes (sex ratio roughly equals one) in populations of most species. In diploid species, sex ratio is mainly determined through gene balance on sex chromosomes. Comparing the sex ratio in the offspring of various species the obtained results sometimes show a disturbed sex ratio, thus, one sex is missing or appears as rare or sterile and it is commonly the heterogametic sex. Examples of the disturbed sex ratio are found in both common types of heterogametic males (XY or XO), but also in females of birds and butterflies, where female sex is heterogametic (ZW) (HURST & POMIANKOWSKI, 1991).

In most *Drosophila* species, particularly in subgenus *Sophophora*, males are carriers of the sex linked factor known as "sex-ratio" (SR), whose presence in-

creases the number of females in the progeny. A disturbed sex-ratio caused by genetic factors has for the first time been described in *Drosophila affinis* by MORGAN, BRIDGES & STURTEVANT (1925) and later in *Drosophila obscura* by GERSHENSON (1928). DOBZHANSKY & STURTEVANT (1936) describe the departure from equal numbers of males and females in *Drosophila pseudoobscura, Drosophila persimilis, Drosophila athabasca* and *Drosophila azteca*. JUNGEN (1968a) detects the existence of an unbalanced sex ratio in the progeny of a natural population of *D. subobscura*. Furthermore, differences in sex ratio are found between populations of the same species, but from different localities.

"Sex ratio" (disbalance between the sexes), as a particular state of the meiotic drive system, similar to unequal segregation of gametes, is caused by the ability of the mutant chromosome, usually X-chromosome, to stimulate irregular development of sperm which bears the normal homologue, in this case, Y chromosome. Aberrant development, as one of the causes of unbalanced sex ratio, may take place during spermatogenesis, but also during the fertilization process.

The factors that affect irregular segregation can be associated either with autosomes or sex chromosomes (HAUSCHTECK-JUNGEN *et al*, 1987; BIRCHER *et al.*, 1995). Male carriers of these factors in heterozygote condition on one of the sex chromosomes distort the equal numbers of males and females, and are called "sex ratio" males.

An SR male can be defined in two ways (HAUSCHTECK-JUNGEN, 1990): (1) they are males with a high percentage of female offspring, or (2) they are male carriers of the "sex ratio" sex chromosome, which is characterized by the presence of inversions at one of the arms. For example, SR males in the Tunisian *D. subobscura* population carry inversions 2, 3, 5 and 7 on the sex chromosome, and, one of the important characteristics of these SR males is that they possess a heteromorphic sperm (BICHER, 1995).

STURTEVANT & DOBZHANSKY (1936) have given a cytological explanation of this phenomenon, finding that, in primary spermatocyte, X chromosome divides twice, autosomes divide normally, while Y chromosome degenerates during meiosis I. Even in that paper the association of the "SR phenomenon" with the X chromosome inversion was observed. However, the inversion alone is not responsible for the specific behaviour of the "sex ratio" chromosome.

NOVITSKI *et al.* (1965), by comparing the SR males and their wild relatives, have found that meiosis I is carried through normally in the wild type, while an anomaly is found in SR males: X and Y chromosomes divide normally during meiosis I, but in meisis II Y chromosome degenerates, staying on the nonfunctional pole

during anaphase II. However, the "sex ratio" phenomenon is not fully explained by such hypothetical approach about the functional pole. By the use of contemporary cytological methods it has been established that the real cause is the halved number of sperm in SR males compared to normal males (POLICANSKY & ELLISON, 1970).

MATERIAL AND METHODS

The *Drosophila subobscura* individuals were captured during June of 1996 and 1997, at mountain Goč, at Dobre Vode locality, altitude of about 800 m, in a fir-beech forest on traps of fermented fruit. The wild females were individually put on the standard substrate and moved to a new one, to the end of their life cycle. Wild males from the nature were crossed with individual unfertilized females, kept in the laboratory on the standard substrate for a longer time period. These pairs were moved to the fresh substrate three times successively.

The progeny was counted of: 130 wild females of 1996, 106 wild females of 1997 and 130 wild males of each year. The total development was on the standard *Drosophila* substrate at 19°C and ca. 60% humidity.

The sex ratio was expressed via *k*-values, i.e. the ratio of emerged females to the total offspring. Thus expressed, sex ratio values (*k*-values) vary from 0 to 1.

RESULTS AND DISCUSSION

Out of 148 wild females 15 (10%) did not have progeny in the population collected in 1996. In the population of 1997, out of 157 wild females 48 (30%) had no progeny. In cases where progeny was completely absent, females of both wild and laboratory population were morphologically analysed for the presence or absence of ovaria, as well as male germinative cells in spermateca. According to the look of ovaria and the presence of spermatozoids in the spermateca of females, 0.68% of the 1996 population are sterile males, and 7.64% of the 1997 population are sterile males. In a sample of 150 wild males in both years no sterile males were found, but in ca. 4.7% of cases progeny is absent. The reason for this can be unrealized copulation.

In the total progeny of wild females of 1996 females constitute 52.32%, and 51.13% in 1997, while in wild males progeny of 1996 females constitute 50.47% and 49.28% in 1997.

Frequencies of males and females of the natural population within *k*-value classes are presented in Fig. 1. It is characteristic to the population analyzed for two

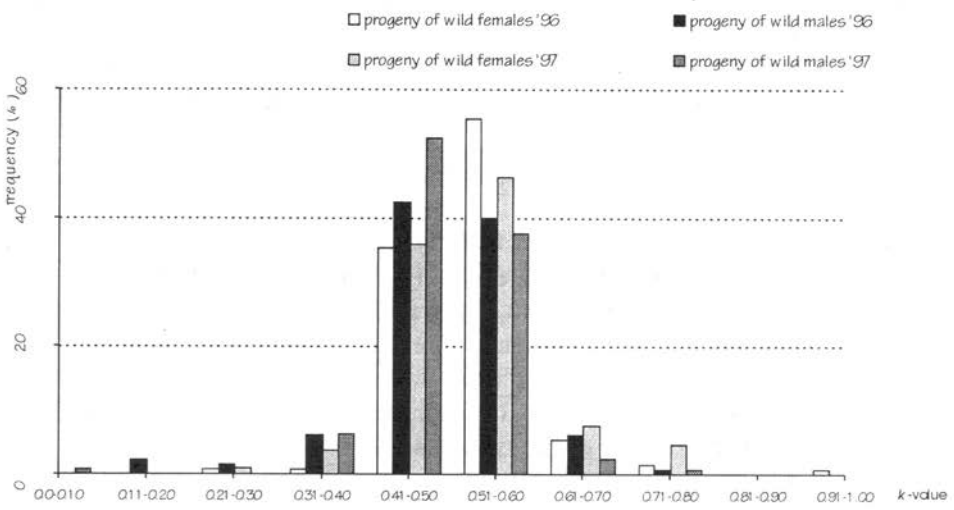

Fig. 1. Frequency of females and males from *Drosophila subobscura* natural population of Goč

years that *k*-valued below 0.30 and above 0.70 are very rare, while those in the 0.41-0.60 range are most frequent, which means that the sex ratio is 1:1.A Kruskal-Wallis non-parametric variance analysis ($p>0.001$) of the distribution of *k*-values of the progeny of wild males and females indicates a statistically significant difference between the distribution of *k*-value classes in the 0.31-0.70 interval, within the progeny of wild males and females, as well as between them, for both years.

JUNGEN (1968b) was the first to clearly observe the existence of the association between the "SR phenomenon" and the inversion on the sex chromosome in the Tunisian *Drosophila subobscura* population. Having in mind the presence of these inversions in earlier Goč populations, which could be correlated with the disturbed sex ratio, indicate a small percentage of these inversions (SAVKOVIĆ, per. com, 1996), which could render this sex ratio expected.

The fact (LOUKAS, 1981) that *D. subobscura* females are not monogamic in natural populations, i.e. 20% of females trapped in nature can mate two times, suggests that analyzed offspring of wild females from mountain Goč may originate from more than one male. Despite the fact that double mating could mask the existence of SR males from nature, data pertaining to the values analyzed for offspring of the wild males suggest the justification of eliminating that possibility.

One of the questions that lends itself concerning the total number of progeny and the progeny of female sex is wether the males have a more numerous progeny if it is predominantly female. In that case, low offspring numbers would produce higher *k*-values. Offspring number classes of wild males are presented in Table I, together, with their average *k*-value during the two years observed. These average numbers in case of *Drosophila subobscura* from Goč do not show statistical significance compared to the total offspring number, which is confirmed by the correlation test ($r=0.37$ for 1996, and $r=0.12$ for 1997, $p<0.05$). A positive correlation indicates that the higher the total of the analyzed offspring the higher the average *k*-values, and vice versa.

Table I

Progeny numbers and the mean *k*-values of *Drosophila subobscura* males from the natural population of Goč

progeny number classes of wild males (1996.)	mean *k*-value	number of wild males	progeny number classes of wild males (1997.)	mean *k*-value	number of wild males
1-30	0.2393	4	1-30	0.3175	3
31-60	0.4451	2	31-60	0.5076	14
61-90	0.5045	4	61-90	0.5299	5
91-120	0.4338	7	91-120	0.4866	5
121-150	0.5087	8	121-150	0.4847	14
151-179	0.4497	13	151-179	0.4718	21
≥180	0.5111	92	≥180	0.4963	66

Numerous investigations of the character of the hybrid sterility and sex ratio in *Drosophila* were led by statements of DOBZHANSKY (1936) that some differences that lead to sterility are located on the X-chromosome, while the autosomes are only apparently involved. Since characteristics and locations of genes that cause sterility in *Drosophila* have not yet been established, the sex ratio phenomenon investigations are still up to date.

In order to understand the factors that maintain the "SR" in natural populations it is necessary to gain insight into the reproductive biology of genus *Drosophila* (WALLACE, 1948; POLICANSKY, 1974; BACKENBACH, 1978; WU & BACKENBACH, 1983; WU, 1983). Thus, one of possible approaches would be an analysis of adaptive value components in adult individuals: female fecundity, male mating success, as well as any other factor produced by differences in male fertility.

REFERENCES

BECKENBACH, A.T., 1978. The "sex-ratio" trait in Drosophila pseudoobscura: Fertility relations of males and meiotic drive. *Am Nat.* 112:97-117.

BIRCHER, U., H. JUNGEN, R. BURCH & E. HAUSCHTECK, 1995. Multiple morphs of sperm were required for the evolution of the sex ratio trait in Drosophila. *J. Evol. Biol.* 8: 575-588.

GERSHENSEN, S., 1928. A new sex ratio abnormality in Drosophila obscura. *Genetics* 13: 488-507.

HAUSCHTECK-JUNGEN, E., W. BURKARD, H. JUNGEN & R. BURCHSCHWALLER, 1987. The loss of Y-sperm in "sex-ratio" (SR) males of Drosophila subobscura is compensated. *Genetica* 74: 27-30.

HAUSCHTECK-JUNGEN, E., 1990. Postmating reproductive isolation and modification of the "sex-ratio" trait in Drosophila subobscura induced by the sex chromosome gene arrangement $A_{2+3+5+7}$. *Genetica* 83: 31-44.

HURST, L.D. & A. POMIANKOWSKI, 1991. Causes of sex ratio bias may account for unisexual sterility in hybrids: A new explanation of Haldane's rule and related phenomena. *Genetics* 128: 841-858.

JUNGEN, H., 1968a. "Sex-ratio" in naturlichen populationen von Drosophila subobscura. *Arch. Jul. Klaus-Stift.* 43: 52-57.

JUNGEN, H.E., 1968b. Inversionspolymorphismus in Tunesischen populationen von Drosophila subobscura Collin. *Arch. Jul. Klaus-Stift.* 43: 3-54.

LOUKAS, M., Y. VERGINI & C.B. KRIMBAS, 1981. The genetics of Drosophila subobscura populations. XVIII Multiple inseminatin and sperm displacement in Drosophila subobscura. *Genetica* 57: 29-37.

MORGAN, T.H., C.B. BRIDGES & A.H. STURTEVANT, 1925. The genetics of Drosophila. Bibliogr. *Genetica* 2: 1-262.

NOVITSKI, PEACOCK & ENGEL, 1965. Cytological basis of "sex-ratio" in Drosophila pseudoobscura. *Science* 148: 516-517.

POLICANSKY, D. & J. ELLISON, 1970. "Sex-ratio" in Drosophila pseudoobscura spermiogenic falure. *Science* 169: 888-889.

POLICANSKY, D., 1974. "Sex ratio" meiotic drive, and group selection in Drosophila pseudoobscura. *Am. Nat.* 108: 75-90.

STURTEVANT, A.H. & T. DOBZHANSKY, 1936. Geographical distribution and cytology of "sex-ratio" in Drosophila pseudoobscura and related species. *Genetics* 21: 473-490.

WALLACE, B., 1948. Studies on sex-ratio in Drosophila pseudoobscura. I Selection and sex-ratio. *Evolution* 2: 189-217.

WU, C.I. & A. BECKENBACH, 1983. Evidence for extensive genetic differentiation between the sex ratio and the standard arrangement of Drosophila pseudoobscura and Drosophila persimilis and identification of hybrid sterility factors. *Genetics* 105: 662-679.

WU, C.I., 1983. Virility deficiency and sex-ratio trait in Drosophila pseudoobscura. I Sperm displacement and sexual selection. *Genetics* 105: 651-662.

ОДНОС ПОЛОВА У ПРИРОДНОЈ ПОПУЛАЦИЈИ *DROSOPHILA SUBOBSCURA* СА ГОЧА, СРБИЈА

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Извод

Код диплоидних врста однос полова је углавном детерминисан генским балансом полних хромозома. Тај однос може бити поремећен и у том случају један пол изостаје, редак је или стерилан и обично је то хетерогамни пол.

Феномен смањења пропорције мужјака у односу на женке, познат као 'sex-ratio' (SR) (несразмера у односу полова), регистрован је код неколико врста рода *Drosophila* и најчешће је, али не и увек, повезан са инверзијама на полним хромозомима.

Анализе сразмере у односу полова потомства женки и мужјака природне популације *Drosophila subobscura* сакупљаних на планини Гочу, на локалитету Добре воде, указују на подједнаку заступљеност јединки оба пола, односно на одсуство SR мужјака.

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