SEXUAL SELECTION CAN REDUCE MUTATIONAL LOAD IN DROSOPHILA SUBOBSCURA

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According to theoretical predictions sexual selection can reduce mutational load through male mating success. Males of good genetic quality should be more successful in matings, compared to the males of low genetic quality, thus in this way females can prevent deleterious alleles to be transmitted to the next generation. We tested this hypothesis through set up of two experimental groups from same genetic pool, where in one group genetic quality was manipulated by ionizing radiation. Within each group opportunity for choosing mates was imposed: males and females had no choice or had multiple choice. Mutational load was measured through the variability of different fitness components: fecundity and egg-to-adult viability. Our results indicate that sexual selection can reduce mutational load, only for fecundity. Group with the presence of female choice exhibited higher fecundity than group in which sexual selection was experimentally eliminated, but only in "irradiated" group. There was no overall difference in egg-to-adult viability between different sexual selection regimes in any of the group. It should be considered that sexual selection can cause sexual conflict, and potential opposite effects of sexual selection and sexual conflict on fitness. Genetic structure of populations, in terms of the level of mutational load, is an important factor which can determinate the role of sexual selection.

Key words: deleterious mutations, ionizing radiation, sexual conflict, fitness

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INTRODUCTION

Mutation is the primary source of genetic variation. Although it represents a fundamental prerequisite for evolvability, most new mutations are deleterious, and every organism carries a load of deleterious mutations (HALDANE, 1937; MULLER, 1950). Mutation is deleterious if it decreases fitness. Besides, mutation can be beneficial if it increases fitness, or neutral with no effects on fitness. While all these effects are possible, most mutations show mildly deleterious effect (LYNCH *et al.*, 1999; CROW, 2000; BAER *et al.* 2007; EYRE-WALKER and KEIGHTLEY, 2007).

Populations are generally under the mutational load, with its level being strongly dependant on the nature of deleterious mutations (mutational effects, degree of dominance), the breeding system of the species and the size of the populations (BATAILLON and KIRKPATRICK, 2000). Whether the fitness increase or decrease in a population depends on the relative rates of beneficial and deleterious mutations, and on the effect of such mutations.

As deleterious mutations decrease fitness, natural selection mainly reduces their frequencies. In addition, sexual selection can push population in the same direction as natural selection. In the past decade Darwin suggestion (1859) that sexual selection may often increase nonsexual fitness is reinvented. The main assumption is that females will have higher fitness than expected, if selection against such mutations is stronger in males than in females (WHITLOCK, 2000; AGRAWAL, 2001; SILLER, 2001). In this way sexual selection can help in reducing the mutational load.

Sexual selection will only reduce the mutational load experienced by females if most new mutations that are deleterious with respect to viability and/or fecundity are also deleterious with respect to male mating success (SHARP and AGRAWAL, 2008). The main assumption is the ability of sexual selection to target alleles with pleiotropic effects on nonsexual fitness. However, there is limited evidence that natural and sexual selection do target the same variation (HUNT et al., 2004; WHITLOCK and AGRAWAL, 2009; HETTYEY et al., 2010). MC GUIGAN et al. (2011) suggested that such evidences can be inferred from several empirical approaches, including the investigation of the alignment of natural and sexual selection focused on specific, well-characterized alleles (WHITLOCK and BOURGUET, 2000; PISCHEDDA and CHIPPINDALE, 2005; SHARP and AGRAWAL, 2008; HOLLIS et al., 2009). In addition, studies of mutation load introduced through a mutagen also proved that sexual selection may target alleles with the pleiotropic effect on nonsexual fitness (RADWAN, 2004; HOLLIS and HOULE, 2011).

However, sexual selection can results in the conflict of interests between the sexes which may lead to antagonistic coevolution. In such a case, sexual selection may act in the opposite direction on nonsexual fitness (HINE *et al.*, 2011). The fact that both increase and decrease in nonsexual fitness have been observed makes it clear that the balance of costs and benefits accrued through sexual selection is unknown (HOLLIS and HOULE, 2011).

If we assume that sexual selection typically acts against deleterious alleles, experimentally removing of sexual selection should decline fitness. In such a case, there will be no possibility for sexual conflict. Therefore, fitness should reflect mutational load of populations, without the influence of sexual selection, as well as the sexual conflict. Experimental manipulation of the level of mutational load and the opportunity for sexual selection (and consequently sexual conflict), should give more precise results about net effect of listed factors on mean fitness of populations.

In order to test the proposed theory of the role of sexual selection in purging genome, we increased the mutational load of treated experimental group of *Drosophila subobscura* using ionizing radiation. We changed the opportunity of sexual selection in both, treated and control group, and measured fecundity and egg-to-adult viability. The use of same initial genetic pool of individuals in establishing these experimental groups gives new insight into a population evolution dynamics.

MATERIALS AND METHODS

The experiments were conducted on a species *D. subobscura*, member of the *obscura* group species. It is a good model system in evolutionary and genetic research since it is genetically well described using several genetic markers (KRIMBAS, 1993; JELIC *et al.*, 2012). Lines used in this study derived from flies collected from Eastern Serbia. After establishing of 10 isofemale lines (IF), each represents a progeny of one individual gravid female, we performed 15 generations of full-sib matings within line. Randomly chosen pairs of F1 progeny from each IF line were parents of the first generation of full-sib (*FS*) mating.

Additionally, 2-3 individual brother-sister mating were made within each line in every generation, according to procedure described in KURBALIJA NOVICIC *et al.* (2012). Progeny of only one pair was randomly chosen to continue the experiment, in order to minimize the loss of IF lines, as in RASIC *et al.* (2008).

The highly inbred IF lines were used to setup two experimental groups: "non-irradiated" (further referred as "control") and "irradiated". Ten replicates were made for each of ten IF inbred lines, within each of experimental group, with the aim to provide enough flies for further experimental procedure. All inbred IF lines and experimental groups were reared on standard *Drosophila* medium (water/cornmeal/yeast/sugar/agar/nipagine as fungicide).

We maintained the "irradiated" experimental group using the half of replicas, where we manipulated genetic quality of randomly selected males (2 to 4-days-old) by inducing new mutations with ionizing gamma radiation with aim to target a wide range of the genome.

Females were not irradiated to avoid maternal effects. The implemented radiation dose was 30Gy (dose rate of 18.12 Gy/h) with the distance from the radiation source of 100 cm. The radiation dose was chosen with the intent to induce mutations with high probability, but not to considerably decrease fertility of males as in PEKKALA *et al.* (2009). The mutational load we used is not based on a few known phenotypic visible mutations, but on the mutations of the genomewide mutations. Although we used induced mutations, rather than spontaneous, they should not substantially change the estimation of effectiveness of sexual election in purging mutational load (RADWAN, 2004). All treatments were conducted under equal and constant laboratory condition at 19°C, approximately 60% relative humidity, light of 300 lux.

Fifty to sixty virgin males were treated per line in total (ten to fifteen males per line every 5 days). Two days after radiation, 4-6 days old males were mated with non-irradiated virgin females of the same age, from the same lines. These lines were labelled as "irradiated". At the same time the half of replicas of inbred lines were maintained as usual (as control group). We began experimental setup with the next generations of lines. Virgin individuals were collected every 24 hours. All flies were five days old at the beginning of the experiment.

We created all possible combinations of monogamous matings between lines within control group, as well as between lines within "irradiated" group. All differences between these two groups can be assigned to new mutations, induced in males which were irradiated in the

previous generation. Every mating combination was repeated ten times, successivelly, enabling enough progeny for the next generation, for assessing the influence of induced mutations, and sexual selection treatment, to the measured fitness components.

Our experimental design allowed us to form the same combinations of matings in control and "irradiated" group, once again, in the next generation. As the aim of this study was to test the role of sexual selection in reducing mutational load, we set up two types of matings in each experimental group.

First type of mating enforced monogamy with experimentally limited the sexual selection (further reffered as S-), where each virgin female was mated to a randomly chosen virgin male. In the second type of mating, five virgin females were placed with five virgin males, so sexual selection was allowed (further reffered as S+). The scheme of matings in this generation is presented on Figure 1.

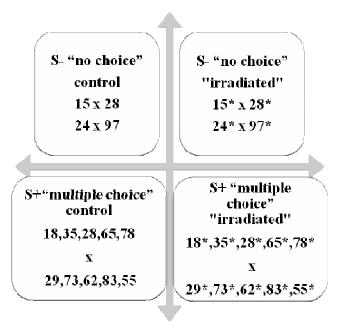


Figure 1. The sheme of matings within each of experimental groups (irradiated and control both, with or without sexual selection regime: S- and S+).

Comment: Numbers present the origin of flies we used (i.e. line 15 was formed by mating female from line 1 and male from line 5; line 15* was formed by mating female from line 1 and male from line 5* (Line 5 whose father was exposed to radiation)).

Five days old virgin males and females were placed to mate. The same number of S+ and S- matings within each of groups (control and irradiated) was used. Four days after mating females were placed in vials separately to lay eggs. For both S+ and S- matings every female was placed on individual substrate. Eggs were counted during three days, by transfering each

female to a new standard medium every 24 hours. A total number of eggs for three days was used as a measure of fecundity.

After counting total number of laid eggs, vials were left for adults to hatch. Egg-to-adult viability was calculated as the percentage of hatched individuals of the total number of layed eggs.

We maintained the control and "irradiated" groups for three generations by random matings of one male and one female. Then we conducted the same types of mating as described before. S- and S+ matings within each group were performed. All experimental groups were set up in the same way, by random placing five days old virgin flies. This generation was labeled as fourth experimental generation.

In both experimental generations males and females after eclosion were separated. The aim was to analyze whether mutations affect sex ratio, considering the large number of genes on X chromosome and potential lethal mutations in males. We presented sex ratio as percentage of males.

Statistical analyses

All data were tested for departures from normality by non-parametric Shapiro-Wilk test incorporated in PAST software (HAMMER *et al.*, 2001). As data for egg-to-adult viability and sex ratio showed deviations from normality, they were arc sin square root transformed. All data showed normal distribution after transformation.

Furthermore, we performed two- and three-way ANOVA (Statistica 8.0) analyzing the effect of treatment, mating system and generation on different fitness components. Figures were done in SPSS 17.0.

After normalizing data we used two-way and three-way ANOVA analysis. As S+ experimental groups had five times more data series, this analysis was possible only by using the average of data for every mating in S+ groups. We calculated the average fecundity for five females, as well as the average egg-to-adult viability and sex ratio for every S+ mating. We had cases when one or more females, from a total of five, did not lay eggs, or died during the experimental procedure. Matings with three or less females were excluded from the analysis.

RESULTS

The descriptive statistics for all measured fitness traits: fecundity, egg-to-adult viability and sex ratio is presented in Table 1.

Fecundity was not significantly different between control and irradiated groups in the first experimental generation. However, difference was significant in fourth experimental generation (F=6.607, p=0.011), where female fecundity was higher in control group compared to the female fecundity in irradiated group. After LSD post hoc analyses we found significant differences between S- control and S- irradiated groups (p=0.002), S+ control and S- irradiated groups (p=0.007), as well as between S- and S+, both irradiated (p=0.02). An interaction of the mating system and treatment is presented on the Figure 2.

It displays significantly different fecundity values for applied mating systems (S- and S+), depending on the level of mutational load. Marginal significance for mating system and treatment interaction confirms these results.

Table 1. Summary statistics for fecundity,	egg-to-adult via	iability and s	ex ratio,	in the first	and fourth
experimental generations					

generation	mating type	experimental	Mean ± S.E.			
		groups	fecundity	egg-to-adult viability	sex ratio	
I generation	S-	control	103.33 ± 5.14	0.79 ± 0.01	0.48 ± 0.01	
		"irradiated"	103.75 ± 4.02	0.78 ± 0.02	0.48 ± 0.01	
	S+	control	91.3 ± 2.13	0.73 ± 0.01	0.47 ± 0.005	
		"irradiated"	94.07 ± 2.25	0.71 ± 0.01	0.48 ± 0.005	
IV generation	S-	control	83.902 ± 3.58	0.78 ± 0.02	0.50 ± 0.01	
		"irradiated"	70 ± 3.63	0.76 ± 0.02	0.50 ± 0.01	
	S+	control	81.89 ± 1.86	0.76 ± 0.01	0.49 ± 0.006	
		"irradiated"	80.08 ± 1.90	0.75 ± 0.01	0.48 ± 0.005	

Results of two-way ANOVA of mating system and treatment effect on fecundity in first and fourth experimental generation are presented in Table 2.

Table 2. Two-way ANOVA of mating system and treatment influence on female fecundity of the first and fourth experimental generations.

Source	d.f.	F	P
I experimental generation			
mating system	1	7.804	0.006**
treatment	1	0.171	0.68
mating system x treatment	1	0.092	0.761
IV experimental generation			
mating system	1	1.697	0.194
treatment	1	6.607	0.01**
mating system x treatment	1	3.746	0.05*

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

Fecundity showed significantly different values between S- and S+ groups in the first experimental generation only. LSD post hoc analysis showed significance between S- and S+ groups within control group (p=0.03), and marginal significance within irradiated group (p=0.07). Fecundity was higher in groups with relaxed sexual selection (S-).

Results of three-way ANOVA of generation, mating system and treatment effect on fecundity are presented in Table 3. We found the significant generation effect, as well as

significant interactions: generation x mating system, and generation x treatment. Female fecundity was significantly higher in the first experimental generation. The generation x mating system interaction showed a different pattern between generations, with significant difference between S+ and S- groups in the first experimental generation (LSD post-hoc analysis p=0.002). The results indicated that females with mate choice opportunity laid fewer eggs than females without choice. No significant differences were found in fourth experimental generation. Patterns of mating systems in both generations are presented in Figure 3.

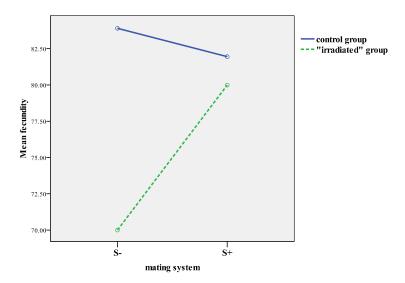


Figure 2. Mean fecundity of S+ and S- matings of irradiated and control groups in fourth experimental generation.

Table 3. Three-way ANOVA of generation, mating system and treatment influence on fecundity

Source	d.f.	F	P
generation	1	59.601	0***
mating system	1	1.888	0.17
treatment	1	1.625	0.203
generation x mating system	1	8.964	0.003**
generation x treatment	1	3.69	0.05*
mating system x treatment	1	2.076	0.15
generation x mating system x treatment	1	0.932	0.335

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

Generation x treatment interaction showed different patterns between generations. The significant difference was obtained between control and "irradiated" females in the fourth experimental generation (LSD post hoc p=0.02). Females from control group had higher fecundity compared to females from irradiated group (Figure 4).

The results of two-way ANOVA of mating system and treatment influence on egg-to-adult viability of the first and fourth experimental generations are shown in Table 4.Contrary to fecundity results, egg-to-adult viability did not show significant effect of the increased level of mutational load. We detected the significant effect for mating system in the first experimental generation only. The same trend, but not significant, was observed in fourth experimental generation. Egg-to-adult viability was higher in the groups with relaxed sexual selection, regardless of the level of mutational load. LSD post hoc analysis showed significant differences between S+ and S- groups in control group (p<0.001) and in irradiated group (p<0.001). These results are presented in the Figure 5.

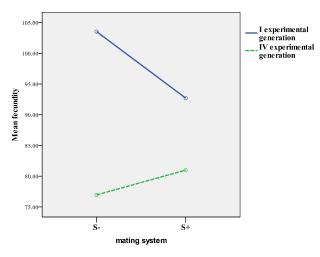


Figure 3. Mean fecundity of S+ and S- groups in the first and fourth experimental generations.

Table 4. Two-way ANOVA of mating system and treatment influence on egg-to-adult viability in the first and fourth experimental generations.

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Source	d.f.	F	P	
I experimental generation				
mating system	1	27.423	0***	
treatment	1	1.756	0.187	
mating system x treatment	1	0.034	0.853	
IV experimental generation				
mating system	1	3.437	0.065	
treatment	1	0.07	0.791	
mating system x treatment	1	0.018	0.894	

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

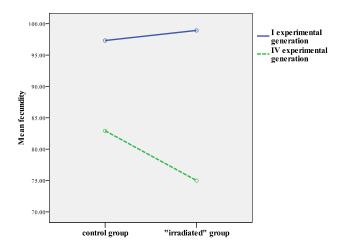


Figure 4. Mean fecundity of irradiated and control groups in the first and fourth experimental generations.

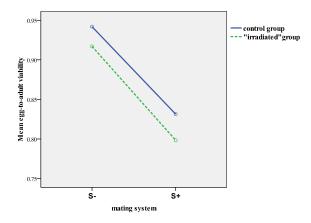


Figure 5. Mean egg-to adult viability of S+ and S- of control and irradiated groups in first experimental generation.

The results of three-way ANOVA of generation, mating system and treatment influence on egg-to-adult viability of the first and fourth experimental generations are shown in Table 5. In contrast to fecundity, egg-to-adult viability did not show significant variation between generations. However, significant results were obtained for the mating system (F=24.42, p<0.001) and *generation x mating system* interaction (F=4.055, P=0.045).

Although the same pattern was evident in both generations, difference between S+ and S- groups were most pronounced in the first generation (LSD post hoc p<0.001) (Figure 6).

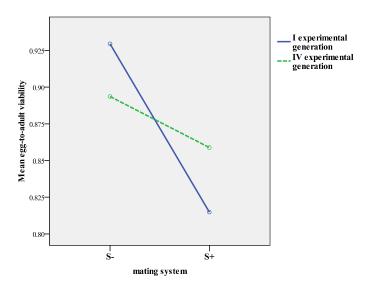


Figure 6. Mean egg-to-adult viability of S+ and S- groups in the first and fourth experimental generations.

The results of three-way ANOVA of generation, mating system and treatment influence on percentage of males are shown in Table 6. The percentage of males was calculated as the proportion of males from total number of survived individuals. There were no significant results within experimental generations, separately. The difference was obtained only between generations (Table 6), with the increased proportion of males in fourth experimental generation in comparison to the first generation (Figure 7). Neither mating system nor treatment had effect on the sex ratio among offspring.

Table 5. Three-way ANOVA of generation, mating system and treatment influence on egg-to-adult viability.

Source	d.f.	F	P
generation	1	0.282	0.596
mating system	1	24.442	0***
treatment	1	1.485	0.224
generation x mating system	1	4.055	0.045*
generation x treatment	1	0.294	0.588
mating system x treatment	1	0.055	0.815
generation x mating system x treatment	1	0	0.99

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

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Lable b. Three-way	ANUVAOT	oeneration mati	no system ana	l treatment intluenci	e on percentage of males.

Source	d.f.	F	P
generation	1	6.44	0.012*
mating system	1	1.932	0.165
treatment	1	0.016	0.898
generation x mating system	1	0.399	0.528
generation x maning system generation x treatment	1	0.039	0.844
	1	0.004	0.952
mating system x treatment generation x mating system x treatment	1	0.84	0.36

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

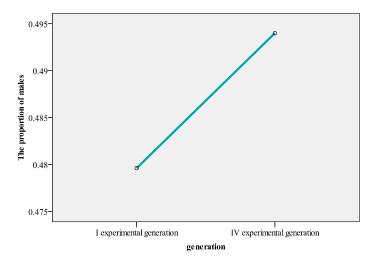


Figure 7. The proportion of males in the first and fourth experimental generations.

DISCUSSION

In the present paper we aimed to test the role sexual selection in reduction of mutational load. Within that framework, we designed the experimental setup where we increased the mutational load of treatment experimental group using ionizing radiation. Then, we change the opportunity of sexual selection (mate choice and non mate choice system) in both, treated and control group using the same initial genetic pool of individuals. Two experimental generations were used in order to minimize the amount of linkage disequilibrium generated through the

mutagenesis procedure (WHITLOCK and AGRAWAL, 2009). Also, in this way we included the potential influence of our experimental design (ie heterotic effect) on fitness measures.

The results of present study failed to confirm the positive role of sexual selection in reducing mutational load through both fitness components measured: fecundity and egg-to-adult viability. The main reasons for such results include the complex genetic basis of fitness components, the complex relations between them, and complexity of action of sexual selection. Furthermore, the overall effect of natural selection and sexual selection on total fitness is very difficult to measure. In addition, in most species with sexual reproduction, the presence of sexual selection involve the existence of sexual conflict. Males and females do not always share the same evolutionary interests, and benefits to members of one sex can result in costs for the members of the opposite sex (ARNQVIST and ROWE, 2005). In this way, the benefits of sexual selection in reducing mutational load can be masked by sexual conflict. Also, as population-level performance is thought to be determined primarily by female fitness in most species (SHARP and AGRAWAL, 2008), any conclusions should be done very cautiously.

The results of this experiment indicate that sexual selection can have the positive role in reducing mutational load, only for fecundity as a measure of fitness. They were obtained in fourth experimental generation when the effect of induced mutational load on fecundity was clearly shown. That was a reduction of number of eggs laid in irradiated group, compared to control group. Mating system x treatment interaction indicate that sexual selection can help in eliminating mutations, but only when their amount was increased. On the contrary, it seems that sexual selection has a negative influence on fecundity, because females from control group with relaxed sexual selection had higher fecundity.

The same pattern of negative influence of sexual selection on fitness was obtained for fecundity in the first experimental generations, as well as for egg-to-adult viability in both experimental generations, independently of the irradiation effect. That could be explained by the existence of sexual conflict in this species. While sexual conflict is more described and analyzed in polyandrous species, there are many examples of monogamy, which can be for or against the interests of one or both sexes (HOSKEN et al., 2009). D. subobscura is considered as monandrous species (HOLMAN et al., 2008), although polyandry was observed in some populations (KRIMBAS, 1993; MARKOW and O'GRADY, 2005). Generally monandry can exist in populations due to benefits which females gain from mating only once or, most probably, as a consequence of male suppression of female remating (HOSKEN et al., 2009). Unless D. subobscura provides another rare example in which monogamy benefits females, it seems more likely to be a consequence of male suppression of female remating (IMMONEN et al., 2009). While it would be easiest to test these hypotheses by monandrous and polyandrous matings for the females from same species, so far published populations analyzes of D. subobscura indicate that female remating in laboratory conditions in this species was not obtained (HOLMAN et al., 2008; LIZE et al., 2012).

In contrast to experiments that questioned the role of sexual selection in reducing mutational load (HOLLIS and HOULE, 2011; HOLLIS *et al.* 2009; MC GUIGAN *et al.* 2011; ARBUTHNOTT and RUNDLE, 2012), in polyandrous species, we assumed that the use of monandrous species would give more clear results considering the role of sexual selection, without influence of sexual conflict. As females were mated with males (were placed with males to mate) only during three days, we even excluded the potential polyandrous matings in sexual selection groups, because they were never obtained in laboratory conditions. It seems that females and males in *D. subobscura* differ in their mating optima.

Females from groups with relaxed sexual selection (S-) had no choice, and matings occurred in most of the cases. Females from S+ groups had choice, but competition of males was also present. So mating success of males was a result of interaction of female choice and male competition. If females are primarily monandrous, males will fertilize most or all of the eggs of each female they copulate with. There should be no expected to find the differences in fecundity between females in S+ and S- groups. However, as males mate several times, females from S+ matings could be fertilized by the same male. In many species, ejaculate size decreases with the number of male copulations, suggesting that the number of sperm and its replenishment are limited (ELZINGA et al., 2011). It will be still beneficial for the males to mate with subsequent females to increase the number of their offspring. For females, in contrast, mating with an already-mated male can be detrimental in terms of fewer sperm, prolonged duration of the copulation, increased risk of unsuccessful fertilization, or shorter lifespan (BAILEY and NUHARDYATI, 2005; HUGHES et al., 2000; JONES et al., 2006; LAUWERS and VAN DYCK, 2006). The question is whether this possibility in a sexual selection groups can have such an effect. If so, the opposite results for fecundity in the irradiation treatment can be explained only by reduction of male fitness (as male mating success) in S- group that exceed a reduction of fitness caused by potential successive matings of males in S+ groups.

Although such effect could be avoided with different operational sex ratios, male-biased operational sex ratio would imply an elevated risk of competition among males, which further can lead to conflict. Increased courtship activity at a male-biased operational sex ratio hass been shown to reduce reproductive fitness in *Drosophila melanogaster* (HOLLAND and RICE, 1999; FRIBERG and ARNQVIST, 2003). It seems that sexual conflict is inevitable when sexual selection acts.

Unlike the experiment of RADWAN (2004), where egg-to-adult viability was substantially higher in a sexual selection treatment, our experiment failed to obtain this difference. It is possible that mutations affecting viability were removed in previous generation, as in Radwan's work. This is possible since ionizing radiation induces a range of mutations, from point mutations to chromosome aberrations (reviewed by EVANS and DE MARINI, 1999). Some of them can be highly deleterious and consequently rapidly eliminated from populations. Other mutations can remain in populations. One of the reasons could be if they do not affect mating success, so the influence of sexual selection in eliminating mutational load cannot be detected. Although we assumed that induced mutations affect the sex ratio, obtained results are in accordance with those for viability. As viability was not decreased, it was expected the equal number of males and females, as in control group.

Our results found a net benefit of sexual selection. Even though they refer only to fecundity, we can conclude that the effect of sexual selection in reducing mutational load can be important when mutation rate is substantially increased. Sexual selection was effective in removing mutations that were induced by ionizing radiation. As control group certainly carried some level of mutational load, decrease in fecundity in irradiated group was a result of higher level of load. Induced mutations showed different effects on used measures of fitness. It seems that influence of sexual selection on fitness can vary, depending on the used fitness measure, number and type of mutations, genetic structure of populations. Still remains to explore the conditions in which the genetic load, caused by mutations, is sufficient for sexual selection to overcome sexual conflict.

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SEKSUALNA SELEKCIJA MOŽE DA REDUKUJE MUTACIONA OPTEREĆENJA KOD Drosophila subobscura

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Izvod

Prema teorijskim očekivanjima seksualna selekcija može smanjivati mutaciona opterećenja u populacijama, preko uspešnosti mužjaka u parenju. Mužjaci koji su boljeg genetičkog kvaliteta bi trebalo da budu uspešniji u parenju od mužjaka lošijeg genetičkog kvaliteta. Na taj način bi ženke mogle da smanje prenošenje štetnih alela u sledeću generaciju. Ova hipoteza je testirana uspostavljanjem dve eksperimentalne grupe od istog genetičkog pula jedinki, pri čemu su u jednoj mutacije indukovane jonizujućim zračenjem. Unutar svake grupe je nametnuta mogućnost izbora u parenju: mužjaci i ženke nisu imali izbor, ili su imali višestruki izbor. Mutaciona opterećenja su merena preko dve komponente adaptivne vrednosti: fekunditeta i preživljavanja od stadijuma jaja do adulta. Dobijeni rezultati ukazuju da seksualna selekcija može imati uticaj na smanjivanje mutacionih opterećenja ali samo za fekunditet. U prisustvu seksualne selekcije su vrednosti fekunditeta bile veće u odnosu na vrednosti koje su dobijene kad je seksualna selekcija eksperimentalno uklonjena, ali samo u okviru "ozračene" grupe. Razlike u preživljavanju od jaja do adulta između različitih režima seksualne selekcije nisu dobijene ni u jednoj od grupa. Kako seksualna selekcija često uzrokuje i seksualni konflikt, treba uzeti u obzir njihovo potencijalno delovanje u suprotnim pravcima na adaptivnu vrednost. Genetička struktura populacija, koja podrazumeva i veličinu mutacionih opterećenja, može biti važan faktor od koga će i zavisiti delovanje seksualne selekcija na adaptivnu vrednost.

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